C. OVERGAARD NIELSEN

STUDIES
ON
THE SOIL MICROFAUNA

II
THE SOIL INHABITING NEMATODES

NATURHISTORISK MUSEUM, AARHUS
DANMARK, 1949

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C. Overgaard Nielsen

Reprinted from "Natura Jutlandica" vol. 2, 1949

Forsvaret finder sted tirsdag den 28. juni 1949 kl. 14 i universitetsannekset, auditorium A, Studiestræde 6 o. g.

Denne afhandling er af det matematisk-naturvidenskabelige fakultet antaget til offentlig at forsvares for den filosofiske doktorgrad.

København, den 15. marts 1949.

J. C. JACOBSEN
b. a. dec.

Copyrigth
NATURHISTORISK MUSEUM
Aarhus Denmark

Printed in Clemenstrykkeriet I/S,
Aarhus

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PREFACE

When, in 1942, I started an investigation on the ecology of freeliving nematodes of the soil it was apparent that knowledge of this group was very scanty. Indeed, several studies had been made on soil nematodes but mostly from other points of view than those in which I was especially interested. A great number of species had been described from soil, and certain aspects of the qualitative distribution seemed to be known. However, the quantitative relations lagged much behind and apart from the genus *Rhabditis* and the plant parasitic species among the *Tylenchinae* almost nothing was known as to the food requirements of the typical soil nematodes (to which *Rhabditis* does not belong). An evaluation of the importance of nematodes in soil biology could not be made because their n u m b e r was unknown (the paper by *Franz* (1941) was not known to me at this time), because their n u t r i t i o n was unknown (apart from occasional observations of gut contents in single individuals, statements which cannot be employed for a systematic study of the question, for this purpose an experimental verification must be insisted upon), and because their r e s p i r a t o r y m e t a b o l i s m was completely unknown. Their moisture relations had been mentioned by several authors but in manuals and textbooks general agreement was not present, often nematodes were considered a group having the same fundamental requirements as mites and collembola. In addition the s i z e of nematodes had never been taken into consideration. Of course, thousands of measurements had been made of nematodes, but the measurements had not been converted to w e i g h t, nor had the animals ever been weighed directly, and the scarce quantitative considerations were based on numbers. This procedure will never be successful when it is realized that the largest nematode known to me from the soil is ca. 2500 times larger than the smallest species, while a size difference of 500 times is common within species of a single sample. It is apparent from the above that the integration of these different factors involves several steps, and that the main stress must be placed upon the c o m m o n species. As a consequence only part of my material has been utilized and all systematic questions have been postponed to later publications. For practical purposes nematode taxonomy is fairly simple (apart from technical difficulties) and the species are satisfactorily defined (with a few exceptions).

From a critical and theoretical point of view, however, much is still to be done,

experimental data of the range of variation being especially needed. Physiological and biochemical questions are numerous too, however, the possibility of axenic culture (culture in absence of other organisms) or even culture in synthetic media is necessary to solve several of them.

The investigations upon which this paper is based were carried out partly in Molslaboratoriet (the Mols Laboratory) belonging to Naturhistorisk Museum (Museum of Natural History), Aarhus and Institut for almindelig Zoologi (Institute of General Zoology) (formerly Histologisk-embryologisk Institut), Copenhagen.

My most sincere thanks are due to the Director of the Naturhistorisk Museum, *H. M. Thamdrup*, Ph. D. for placing the Laboratory at my disposal during the long and short visits to Mols and to the Laboratory for having paid my travelling expenses during the years 1945—48.

In the Institut for almindelig Zoologi I owe much gratitude to my late chief, professor *C. M. Steenberg*, Ph. D., my former chief, professor *R. Spärck*, Ph. D. and my present chief, professor *H. V. Brøndsted*, Ph. D., for the interest they have taken in my investigations and the liberality they have shown in allowing me to spend so much time on the subject. Special thanks are due to professor *Spärck* who made it possible for me to spend a year in Zoofysiologisk Laboratorium (the Zoophysiological Laboratory).

The well known hospitality of this institute was also conferred upon me during my stay there, and my sincerest thanks are due to all the persons employed there, especially to professor *P. Brandt Rehberg*, Ph. D. and to *E. Zeuthen*, Ph. D. Dr. *Zeuthen's* patience, helpfulness and comradeship during this year deserve special thanks.

Since the start of my investigations I have had innumerable discussions with *T. Weis-Fogh*, M. Sc. I owe him much gratitude for this and for valuable critiscism, suggestions and fine comradeship.

Last but far from least I thank Mrs. *Inger Braase* for valuable help in typewriting my manuscript, my wife *Ellinor Overgaard* for help of several kinds and my friend *A. Macfadyen*, M. A. (of Oxford) for having read the manuscript and suggested innumerable corrections and linguistic improvements.

I have obtained financial support for carrying out the field work from *Japetus Steenstrup's* Legat, for which help I beg to receive my sincere thanks.

1. INTRODUCTION

The soil is a complex of mineral and organic particles, water (with dissolved inorganic and organic substances), and air. This complexity implies that the soil may satisfy the most diverse ecological requirements and thus harbour a most diversified fauna.

In order to review this fauna from an ecological point of view it is necessary to arrange the different members according to some principle. It might seem reasonable to represent the dependence of the soil fauna upon the living and dead organic surroundings by a chart of food cycles, however, when trying to do this it rapidly appears that our knowledge of the food requirements of a great number of important soil organisms is far too scanty to allow such a procedure (see e. g. *Jacot* (1936)). So many blanks occur in the chart, that its value is very restricted. As an example earthworms may be mentioned. Probably these animals were the first soil inhabitants upon which the attention of zoologists was focussed, but nevertheless our knowledge of their nutrition is not sufficient for ecological purposes. If one were to construct a food chain for earthworms it would not be sufficient to know what organic and inorganic matters are ingested, but in addition one must find out what is absorbed and which chemical and physical transformations take place especially in the organic substances in passing the gut, because the casts may be used as substratum or food by other soil organisms.

The purpose of this paper is to present such information concerning the biology and ecology of freeliving nematodes that it becomes possible to estimate their qualitative and quantitative share in the biological processes taking place in the soil and to give a picture of their basic environmental requirements.

The facts which may justify the study of freeliving nematodes in this respect are 1. that they occur in much larger numbers in the soil than recorded by most authors and 2. that several modern manuals stress their positive share in the breakdown of decaying organic matter even though their number was much underestimated. Thus it is reasonable to believe that nematodes may play a rather prominent role in soil processes. It is, however, characteristic of most treatments of nematodes in manuals of soil science, that facts are very scanty while suggestions are numerous.

During the attempt to follow this line of research several difficulties were met with — expected as well as unexpected. Some of them proved insurmountable at the moment, while others were overcome more or less satisfactorily.

2. HISTORICAL SURVEY

Our knowledge of freeliving nematodes dates from ancient times; already 1656 *Borel* knew the vinegar eel *(Anguillula aceti)*, however, special attention was not paid to them until 1849 when *Czernay* published his monograph. During the succeeding years they were more intensively studied by scientists such as *Dujardin* (1845), *Diesing* (1851, 1861), *Carter* (1859) and *Eberth* (1863) so that in 1865 about 80 species of freeliving nematodes were known, most of them, however, marine.

Greater interest was focussed upon the species from soil and freshwater in the work of *Bastian* (1865) who described 20 new genera and about 100 new species. Subsequently several authors published investigations (mainly morphological) on nematodes. An important impetus was given by *Bütschli* (1873) who described 61 species from soil and freshwater, about 30 of the species being new to science, later on he published several other papers on nematodes.

De Man opened a new epoch when in 1876 he published a treatise on soil nematodes. He mentions 50 species, the greater part being new. Two other important investigations were published by him (1880, 1881) before his great monograph (1884). In this pioneer work 143 species are described, keys are given for the determinations and most of the descriptions are accompanied by excellent figures greatly facilitating identification. It must be stressed that a wealth of biological and ecological information is presented, so that this work may be considered the first ecological treatise of the soil and freshwater nematodes. The monograph was later on followed by a long series of shorter papers (especially 1889, 1906, 1907, 1912, 1917).

Diem (1903) inaugurated the study of the soil fauna as an entity and was aware of the nematodes as a component of the soil fauna proper, however, his quantitative methods were far too coarse to give a true picture of the detailed composition of the microfauna although many important facts were stressed by him. From the point of view of nematodes the quantitative results are without value because only the larger species (mainly *Dorylaimus spp.)* were obtained by his methods (direct manual sorting out of the fauna).

During the succeeding years the study of the arthropod component of the soil macro- and microfauna was advanced considerably through the technical improvements of *Berlese* (1905) which were later on further elaborated by several others (see *Forsslund* (1943)). However, the study of the nematode fauna of the soil

lagged very much behind, because these animals were not isolated by means of the apparatus used for arthropods.

In spite of the lack of automatic methods for extracting the nematode fauna of the soil the interest in this group of soil inhabitants did not decrease. In arthropods the main interest was focussed upon the qualitative and quantitative distribution, while in nematodes the attention of the investigators was especially attracted by the fact that certain nematodes were able to become severe pests in cultivated plants. Especially the papers of *Marcinowsky* (1906, 1909) are important in this respect and they were followed by a large number of investigations, the interest of the authors especially being directed towards the *Tylenchinae*. To day this group is the only where knowledge is at all adequate. I shall not go further into details in this special branch of nematode biology which to a large extent has its own problems and methods, but will only mention, that much of our present knowledge has been summarized in several manuals among which may be mentioned those of *Chitwood* and *Chitwood* (1937) and *Filipjev* and *Schuurmans Stekhoven* (1941).

The line developed by *De Man* was not neglected by zoologists even if the study of the plant parasitic species was mainly carried out by agricultural laboratories. The purely freeliving species were the subject of many smaller studies, biological as well as taxonomic. *Ditlevsen* (1911) recorded 31 species from Danish soils, some of them being new to science. *Brakenhoff* (1913) found 52 species (2 new to science) in the neighbourhood of Bremen, *Menzel* (1914) studied the nematode fauna of alpine areas (Switzerland) and especially the fauna of moss cushions and rosette plants also giving valuable informations as to nutrition and other biological problems. 1920 he published a paper on the nutrition of freeliving nematodes, in which it is shown that *Mononchus* and others are predators. *Steiner* (1913, 1914) especially investigated the freeliving nematodes of Switzerland, but later on he published several zoogeographical papers containing material from very remote parts of the world.

Micoletzky (1921) wrote a very large monograph of the freeliving nematodes of soil which is still of value to workers on this subject. Besides presenting his own material (11 767 specimens) he reviewed as far as possible the European species and extra-european genera, giving keys for the identification. Much biological information is given which, however, is rather scattered, difficult to find and difficult to synthesize. It is to be regretted that he does not state how his samples were collected and how large they were, with the result that his quantitative statements are of restricted value. In the taxonomic part of the paper he regards the absolute and relative measurements as significant specific characters, and on this basis several species and different degrees of sub-species are described which cannot be maintained but must be considered individual modifications.

In addition to this work he published several others, amongst which one (1925) is devoted to freshwater and marsh nematodes from Denmark. Here he gives an important study of the permanently water-logged localities at borders of lakes etc. From this type of locality he enumerates many freshwater species as well as species otherwhere also occurring in soil.

In Belgium *De Coninck* published a large number of valuable papers most of them concerned with smaller faunas or single species of nematodes, especially interesting, ecologically, is his paper of 1930, where qualitative and quantitative differences between different biotopes are discussed.

Franz and *Beier* (1942) and *Franz* (1942) have studied the soil nematodes in Austria. *Franz*' papers are outstanding in that he was especially investigating the quantitative distribution of nematodes, thus obtaining the largest numbers per spuare unit recorded up till then and of the same order of magnitude as those given by *Stöckli* (1943) and those found in this paper. The seasonal variation of the nematode fauna was studied by *Seidenschwarz* (1923), he reached the conclusion that marked fluctuations in numbers occur, but this has not been confirmed by later authors.

Some other aspects of the biology of soil nematodes must be mentioned. All the quantitative investigations mentioned above were based upon a simple sedimentation and decantation technique which in most cases yields highly unreliable results, as is seen from the small numbers. This method has been especially elaborated by *Franz* (1. c.) and *Stöckli* (1. c.), so as to be completely satisfactory although time-consuming. For the history of the quantitative concept of nematode populations of the soil see *Stöckli* (1. c.).

Special features of the activity of nematodes have been studied by several authors. *Maupas* gives a very valuable study of the post-embryonic development (1900) and reproduction (1901) of some soil species. The nutrition has been studied systematically in *Rhabditis* and a few other species *(Hilgermann* and *Weissenberg* (1918), *Dotterweich* (1938), *Ludwig* (1938)). It was found that the food consists of bacteria. In most other nematodes (except the plant parasitic species) the question of nutrition has still not been satisfactorily investigated, consequently the modern concepts of the importance of nematodes in nature are extremely vague. From an ecological point of view we know from *Franz* (1. c.) and *Stöckli* (1. c.) that nematodes occur in the soil in numbers ranging from some thousands to some millions per sq. m., but how they live, and what they feed upon is practically unknown in most species and the same applies, of course, to their importance, if we are not to resort to mere speculation.

Regarding geographical distribution an overwhelming difficulty is met with, namely that the fauna of Europe, Africa and parts of Asia was mainly investigated by zoologists using European literature based on the standard works mentioned

above, while the fauna of America and Australia was investigated by people using *Cobb's* papers on the American fauna. It is greatly to be regretted that *Cobb* disregarded the European literature, thus creating a complete confusion of the nomenclature which has not yet been solved. *Micoletzky* (1921) has proved that several af *Cobb's* species are identical with species described by European authors, later several others have correlated the two nomenclatures for other species, however, much has still to be done, and the whole problem of the geography of freeliving nematodes is very difficult to discuss. Some indications are at hand, that most species are cosmopolitan. (Thus the papers by e. g. *Micoletzky* (1921) and *Johnston* (1938) show that several species are common to soils of Europe and Australia). On the other hand some well defined and characteristic species have never been found outside the American continent.

Summing up it appears that the qualitative composition of the soil fauna is well known in some localities outside Denmark, while the quantitative statements in the literature are unreliable, the numbers being much too low apart from those given by *Franz* (1. c.) and *Stöckli* (1. c.) from localities in Austria and Switzerland. In addition the quantitative relations have not been stated in terms of weight, apart from rather loose suggestions by *Cobb* and a few others (e. g. *Stöckli* (1946)). Seasonal variations were only distinct in the locality investigated by *Seidenschwarz* (1. c.). The faunas of different localities have been compared by several authors, however, an interpretation of the facts is difficult because edaphic as well as vegetational differences are involved. Nevertheless it seems that certain species are confined to definite types of locality while most species are eurytopic. The vertical distribution has not been especially studied but it seems to correspond to that of most other soil microorganisms (see e. g. *Franz* (1942)). The moisture relations are known in principle but often neglected. The respiratory metabolism has never been investigated. The nutrition is only known from occasional observations. Culture experiments with defined food have only been performed with plant parasitic species, *Rhabditis spp.* and *Diplogaster spp.* (see e. g. *Dougherty* and *Calhoun* (1948)), the nutrition elsewhere being unknown or statements being unreliable. The reproductive rate is known from experimental conditions (especially *Maupas* (1901)). The importance of nematodes has been discussed on the basis of unreliable suppositions only.

3. MATERIAL, METHODS, AND NOMENCLATURE

1. Material.

When studying the ecology of a component of the microfauna two essentially different procedures are possible: 1. to investigate in great detail the qualitative and quantitative distribution of the group in a restricted area (e. g. some few

sq. m.) and 2. to investigate a variety of biotopes on a wider scale. In order to give the reader an understanding of the general composition and selection of material it is necessary to state that my investigations were started in 1942. However, at this time no technical facilities were at my disposal, and the samples were examined by means of a simple and often unreliable sedimentation and decantation method. At the time when technical improvements had been worked out (1945), however, on account of the experience already gained, it had become evident to me that qualitative and quantitative differences in the composition of the fauna within a restricted area could rarely be demonstrated.

Thus it was decided to carry out an investigation of the nematode fauna in different localities. Here a difficulty was met with: the localities had to be defined in a reproducible way. On account of the great work involved in the sorting out and identification of the animals a close inquiry into the physical and chemical nature of the soils of different localities could not be undertaken. Thus it was most necessary to carry out the investigations in localities which could be characterized in descriptive terms, the value of the investigation in this way mainly being confined to geographical areas where analogous localities are present. In northern and central Europe several localities with this property are met with. In this way one advantage is achieved: so many localities can be investigated and so large a quantitative material obtained, that mere experience can give the clue to the basic phenomena deciding the type of distribution, and a fairly clear picture of the physical and chemical factors the knowledge of which will be of value in future research work. This experience is difficult to obtain in the case of a material from a restricted number of localities, the basic factors easily being overshadowed by less important or incomparable ones, and the restricted material not allowing one to check the conclusions obtained. At this point certain results may be anticipated, *viz.* that many of the soil analyses ordinarily stated in ecological papers are of very small value when applied to the nematode fauna, this is certainly the case with instantaneous measurements of temperature and water content, mechanical analyses, pH etc. Generally the mere static concept of the soil as an environment must be abandoned and more attention be paid to the changes in intensity and the combined effects of factors, because nematodes are so well fitted for living in the most different surroundings that no single factor normally occuring in nature will influence these animals significantly when applied for a short time. In a later chapter these points of view will be further elaborated.

The localities investigated were arranged in two main groups: mineral and organic soils according to the content of organic matter. In temperate climates such a procedure is relatively easy to apply as a first approximation. Under Danish conditions the mineral soils with an organic matter content about 2—10 % are the most important.

The series of mineral soils investigated extends from pure sand practically without admixture of clay or organic matter, via sands with increasing admixture of these two elements to heavy clay soils (on a Danish scale).

The organic soils are represented by different types of raw humus and peat of varying moisture status.

These groups can be quite simply recognized in this country and in order to define the localities more precisely typical vegetation types were always chosen extending from halophilous types from shore beaches via inland-dunes with *Corynephorus canescens*, mosses, lichens etc., *Calluna vulgaris* heaths (on sand and raw humus), different types of virgin and cultivated pastures (dry fields with sand or clay soil), virgin and cultivated meadows (sand or peaty soil), and cultivated fields carrying different crops. From these localities upwards of 350 000 individuals of nematodes were isolated of which ca. 205 000 are included in the tables given here. The area from which most of my samples originate is the grounds belonging to the Mols Laboratory near Femmøller in Jutland. Besides, several samples were taken in western Jutland (in the neighbourhood of Herning) and in the vicinity of Copenhagen. A single series of samples derives from Funen (near Assens). A more detailed description of the localities in Mols is given by *Thamdrup* (1948).

2. Methods.

The sampling was carried out by means of a steel cylinder with cutting edge, area 1 sq. cm., effective height 5 cm. A series of samples were taken in each locality, generally about 10 at a time. In most localities sampling was performed at different seasons of the year. Each sample was placed in a glass tube with tightly fiting cork and stored in a dark and cold place (0—3° C) pending examination. Several of the samples from each locality were extended to a depth of 20—25 cm and divided into as many separately stored samples of 1 cm height in order to get an idea of the vertical distribution of the fauna. In this way it was found that in most localities a sampling depth of 5 cm would yield a very large proportion of the total fauna. However, in some cases the sampling depth on account of another type of vertical distribution had to be extended to the layers 0—10 cm while in a single case (shore beach) it was practically impossible to take samples according to this procedure because the sampling had to be extended about 50—75 cm below the surface in order to obtain the same proportion of the total fauna.

Another type of sample has also been employed: in some localities supplementary material for investigating the qualitative composition of the fauna was obtained by isolating 500 individuals at random from a clod of soil and after determination

of the species their relative importance was calculated. For further details of technique see *Overgaard* (1948 a and b).

From 1945 the extraction of the fauna was performed by means of an apparatus constructed for this purpose *(Overgaard* (1948 a)). In the paper mentioned the efficiency of the extraction was checked in different cases, and it was found that when the samples were treated at once or after storage for upwards of a month at 0—3° C the loss of individuals practically never exceeded 10 %. In this paper the efficiency of the extraction of the single samples is also ca. 90 %. When multiplied by a factor of 10 000 the figures give the number of individuals per sq. m., the numbers thus being minimum values. It must be emphasized that this number in most cases refers to the layers 0—5 cm, but in others to the layers 0—10 cm. the sampling depth being stated for each single locality.

The technique used for identification is the one mentioned in a previous paper (1948 a). All the specimens were paralized by heat before identification.

In order to measure the weights of the animals partly for respiratory measurements and partly for evaluating the weight of the fauna per unit area, direct weighing had to be excluded on account of the great errors which would be introduced by weighing generally several thousands of individuals in order to obtain a couple of mgs, an error partly due to small weighing accuracy and partly to the water transferred with the animals. Another procedure, the measurement of the N-content *(Brüel, Holter, Linderstrøm-Lang* and *Rozits* (1946)) was precluded partly on account of its rather complicated technique in case of a large material, but mainly because I have considered it more satisfactory—in an ecological paper—to use a method which can be used by field ecologists without the refined working facilities available in special laboratories. and which could easily be reproduced in the field with a satisfactory accuracy.

The following method was worked out on basis of the fact that the cross-section of nematodes is strictly circular (with the exception of *Bunonema* and a few species not occuring in my material).

a. For respiration measurements.

Given an absolutely cylindrical hypothetical nematode, length 1332 μ, diameter 66.7 μ. At the magnification used an optical sagittal section of this animal represents a square 100×5.0 mm = an area of 500 mm^2.

This area drawn on a particular type of paper by means of a "camera lucida" weighs 45.6 mg, the volume of this nematode being $\pi r^2 l = \pi \times 2.5^2 \times 100 =$ 1960 μ l. This hypothetical nematode is used as a standard.

Example:

Wishing to know the relative volume of an individual of say *Mononchus papil-*

latus 1693 μ in length the specimen is drawn at the same magnification on the same type of paper and the weight of the outline-drawing turns out to be 53.2 mg.

The length of the animal can be measured accurately along the midline (127 mm), the diameter cannot because it is different at different points of the body, but the mean diameter can be calculated:

Standard: $100 \times 5.0 = 500$ mm^2 $\sim$ 45.6 mg.

M. papillatus: $127 \times 2r = y$ mm^2 $\sim$ 53.2 mg (1)

$$y = \frac{53.2 \times 500}{45.6} = 583 \text{ mm}^2 \quad (2)$$

$$2rl = 2r \times 127 = 583 \text{ mm}^2 \quad (3)$$

$r = 2.295$ mm.

relative volume of *M. papillatus* $= \pi \times 2.295^2 \times 127 = 2100\ \mu 1$ (4)

and hence the

$$\text{real volume} = \frac{2100}{1960} \times 33.35^2 \times \pi \times 1332 = 4980729\ \mu^3.$$

Putting the specific gravity at 1.02 as found by means of a "salt gradient" we get the weight $5.08\ \gamma \sim 5\ \gamma$. ($1\ \gamma = \frac{1}{1000}$ mg).

b. For calculation of weight per unit area.

A random sample of about 50 young and adult specimens of each species was drawn at the same magnification. The length was measured and—at a larger magnification—the diameter of the animal at the middle of the oesophagus was stated and extrapolated to the original magnification and to the real values.

Subsequently these two measurements were used for calculating the volume.

Example:

The above specimen of *Mononchus papillatus* gave the following result: $\pi r^2 l = \pi \times 31.0^2 \times 1690 = 5099643\ \mu^3$. A specific gravity of 1.02 gives the weight $5.20 \sim 5\ \gamma$.

By the latter process values are obtained which are constantly a little greater than those obtained by the former procedure, generally they are about 2 % larger but in case of species with a very slender tail (*Dorylaimus longicaudatus, Prismatolaimus dolichurus, Monhystera filiformis, M. vulgaris, Teratocephalus terrestris, Rhabditis filiformis, Tylenchus filiformis* etc.) the difference may be slightly greater. On account of the many errors always involved in field ecological investigations I have found it sufficient to put the specific gravity = 1.

In both methods errors are involved, in the first case they are believed to lie within $\pm$ 10 %—and when the procedure is accurately performed they are insignificant in practice, as will be seen from the curve fig. 15, the points being distribut-

ed just as evenly as in the case of larger animals where the weighing procedure is employed and as in smaller animals where the measurements are based on N-determinations (e. g. *Zeuthen* (1947)), the individual variation in 0_2—consumption always exceeding the error of the method.

Two facts deserve mention: All measurements must be made on objects the longitudinal axis of which is perpendicular to the direction of the axis of the microscope, and, still more important: measurements must be made without a coverslip because the diameter and consequently the "weight" is increased on account of pressure deformation during the continued evaporation. In the specimen of *M. papillatus* mentioned above the following measurements were obtained when using a coverslip:

Without coverslip:			diam. 62 μ	"weight"	5 γ.
With coverslip:					
at time	0 min.	-	66 μ	—	5 γ.
	5 -	-	70 μ	—	7 γ.
	10 -	-	76 μ	—	8 γ.
	20 -	-	92 μ	—	10 γ.

By applying the procedure of weight calculation mentioned above (b) to the most important species of soil nematodes the values shown in table 1 were obtained. In all sections of this paper excepting the chapter on the oxygen consumption these values have been used.

Measurement of 0_2-consumption. As far as I know the oxygen consumption of freeliving soil nematodes has never been especially investigated probably on account of technical difficulties in connection with their small size. My measurements were performed by means of the diver-technique *(Holter* and *Linderstrøm-Lang* (1943)). The original technique was not altered to any appreciable extent. For the description of the method the reader is refered to the paper mentioned. Most measurements were made at 16° C. and with divers with a total volume of 9—20 μ l according to the sizes and levels of respiration of the animals. All experiments were performed in such a way that the oxygen consumption did not alter the equilibrium pressure less than 1 cm water pressure per hour. Consequently the number of animals (or size of divers) had to be altered according to species. The duration of the single experiments was very different, varying from two to forty-eight hours.

Some difficulties were met with in getting the animals into the braking pipette used for placing the bottom drop with the animals in the diver. In most cases it was practically impossible to suck up the correct number of animals in a fixed volume of water (generally 1 μ l). The difficulties were overcome by using a hair fixed to a glass rod. By means of this simple instrument it was easy to pick up

Table 1.

species	weight γ	species	weight γ
Alaimus primitivus	0,3	*Monhystera villosa*	0,3
Diphtherophora communis .	0,3	*Monhystera similis*	0,2
Tylencholaimus mirabilis ..	1	*Monhystera vulgaris*	0,2
Tylencholaimus stecki	1	*Monhystera filiformis*	0,2
Dorylaimus limnophilus ...	1	*Rhabditis monhystera*	0,6
Dorylaimus longicaudatus .	5	*Rhabditis longicaudata* ...	0,7
Dorylaimus carteri	2	*Teratocephalus palustris* ..	0,5
Dorylaimus regius	56	*Teratocephalus terrestris* ..	0,2
Dorylaimus rhopalocercus .	4	*Teratocephalus crassidens* .	0,2
Dorylaimus centrocercus ..	3	*Acrobeles vexilliger*	0,5
Dorylaimus obtusicaudatus	10	*Acrobeles ciliatus*	0,6
Dorylaimus tritici	13	*Cephalobus nanus*	0,4
Bastiania gracilis	0,2	*Cephalobus persegnis*	0,6
Tripyla setifera	3	*Cephalobus striatus*	0,5
Tripyla papillata	4	*Cephalobus oxyuroides*	0,5
Prismatolaimus intermedius	0,3	*Cephalobus elongatus*	0,8
Prismatolaimus dolichurus .	0,3	*Panagrolaimus rigidus*	0,5
Mononchus macrostoma ...	5	*Bunonema richtersi*	0,02
Mononchus papillatus	5	*Bunonema reticulatum*	0,02
Mononchus brachyurus ...	5	*Ecphyadophora tenuissima* .	0,1
Ethmolaimus pratensis	0,2	*Tylenchorhynchus dubia* ..	0,5
Achromadora dubia	0,2	*Rotylenchus robustus*	0,7
Wilsonema auriculatum ..	0,2	*Pratylenchus pratensis*	0,3
Wilsonema otophorum	0,1	*Tylenchus davainei*	0,8
Rhabdolaimus terrestris ...	0,2	*Tylenchus filiformis*	0,5
Plectus granulosus	1	*Tylenchus dipsaci*	0,9
Plectus cirratus	1	*Paraphelenchus pseudo-*	
Plectus rhizophilus	1	*parietinus*	0,4
Plectus longicaudatus	1	*Aphelenchoides parietinus* .	0,4
Plectus parvus	0,5	*Criconema rusticum*	0,9

individually the small species as well as the larger ones. Under a binocular microscope the animals were transferred to the braking pipette into which had been sucked the volume of water intended for the bottom drop. When the appropriate number of animals had been transferred to the pipette the volume was adjusted to its correct size by means of another pipette filled with water. Of course the dimensions of the adjusting pipette had to be such that the animals could not pass into it, i.e. the diameter had to be less than 20 μ. Such pipettes were drawn over a microflame.

Another difficulty was met with in measuring the oxygen consumption of very large animals. They often crept up the walls of the diver bulb and touched the NaOH seal, thus creating a water bridge and allowing mixing of the two drops. This was hindered by placing a very loose ball of filter paper below the NaOH seal (of course the ball had to be so loose as to allow the free passage of air).

When an animal creeping up the wall of the diver bulb came into contact with this dry ball it immediately withdrew to the lower part of the diver bulb.

In a few cases the duration of the contact was so prolonged that water was sucked into the filter paper. In these cases the experiments were stopped.

All the ordinary measurements of 0_2-consumption were carried out with washed animals in a tap water bottom drop.

It has often been claimed that most determinations of 0_2-consumption were not performed under natural conditions, either the environment or the physiological state of the objects deviating from those found in nature. Of course, this point of view may be correct; in most cases, however, one has to choose between measurements under circumstances deviating more or less from the natural ones or no measurements at all. To some extent it is, nevertheless, possible to check the influence of certain physical and chemical factors: temperature (and type of temperature variations), light, oxygen tension, pH etc.

As will be shown later biological factors, especially the developmental stage are also of great importance for the level of 0_2-consumption.

The methods of culture for the study of the nutrition of the nematodes were originally based on *Dotterweich* (1938) with some alterations.

A stock solution after *Knop* as modified by *Pringsheim* (1946) was made (KNO_3 0.1 %, $Ca(NO_3)_2$ 0.01 %, K_2HPO_4 0.02 %, $MgSO_4$ $7H_20$ 0.01 %, $FeCl_3$ 0.0001 %). To this solution in a dilution of 1/4 1.5 % agar was added. When cooled down to 60° C. 20 % of freshly prepared potato juice was added and the pH adjusted to 7.4 (brom thymol blue) by means of N NaOH and plates were poured in Petri dishes.

The growth of the cultures was good on this substratum but so many colonies of bacteria and actinomycetes developed in the lower layers of the agar that it was difficult to find the animals in the dishes, because many individuals moved down into the colonies below the surface.

A much more satisfactory procedure consisted in pouring asparagin mannitol agar plates *(Thornton* (1922)) with 2 % of agar instead of 1.5 % after sterilization of the solution (in autoclave at 1 kg/sq.cm for half an hour). The plates were inoculated with a soil suspension of 1 : 100 000 dilution. In a week a dense growth of bacteria covered the plates. Now 30 adult nematodes were transferred to each plate by means of a hair. In this way the growth of the bacteria was restricted to the surface and on account of the somewhat harder agar the nematodes rarely migrated below the surface. Thus it was easy to count the animals every day, but the eggs were difficult to find because their colour coincided almost completely with the colour of the substratum. This method was employed for maintaining a large number of nematodes to be used for experimental purposes.

The cultures increased rapidly in this way, but it turned out that the hatching was a critical stage for some reasons not quite clear.

The detailed examinations of the nutrition of the nematodes were carried out in hanging drops of sterile water with a very dense suspension of a single species of bacteria. The drops were kept in the ordinary moist chambers mounted with vaseline. In order to avoid contamination with bacteria transferred with the animal a special technique was worked out. Eggs were transferred from a culture to water and subsequently washed in a saturated solution of $HgCl_2$ for 15 minutes. After repeated washing with sterile water in sterile pipettes they were taken to the bacterial suspension and the chambers were sealed.

Several inoculations of the sterilized eggs on sterile agar and gelatin plates gave never rise to colonies of bacteria and when the eggs were transferred to the suspensions they hatched readily i.e. 95 %. The hanging drop cultures were used to test the edibility of different bacteria and to investigate the duration of the different developmental stages of the most important species of nematodes.

Also algae were used as food for certain nematodes. These cultures were maintained in glass tubes with *Knop* solution (see above). No attempt was made to obtain pure cultures. Unialgal cultures of *Hormidium flaccidum* were employed in all cases, the results always being compared with controls consisting of the same nematode species in bacterial cultures.

3. Nomenclature.

The following systematic nomenclature was adopted: For nematodes *Schneider* (1939), for higher plants *Raunkjær* (1942), for mosses *Jensen* (1923) and for bacteria *Bergey* (1948).

The ecological nomenclature is very plain and does not require special explanation. The term »biotope« is used in the connection »type of landscape« while »locality« denotes a geographically fixed plot of soil with a homogeneous appearance as regards the nature of soil and vegetation.

4. SURVEY OF THE FAUNA IN VARIOUS LOCALITIES

In this chapter a general presentation of the material from some selected localities is given. As far as possible all the localities are treated identically in order that the materials may be compared directly, however, some deviations from this principle were inevitable.

In the first place an analysis is given of the sandy areas of "the Plain" one of my main localities in rather greater detail than in the case of the remaining localities. By using this procedure I anticipate some general principles with regard to the range of variation of the fauna of different localities in order to give a

preliminary orientation of the position of the single localities in comparison with others. In this way, I hope, the reader may obtain a general picture of the main facts which will be subject to a closer examination in chapters 5 and 6. In addition the Plain may serve as a model for the general set up of the data.

I. MINERAL SOILS

1. The Plain.

One of my main localities is located on "the Plain", a permanent pasture in the grounds of the Mols Laboratory. The Plain is used for grazing and situated on raised *Littorina* ocean floor. Topographically it lies parallel to the shore line about 500 m inland. On the other side it is bordered by the ancient shore line indicated by tall, steep slopes. The greater part of the area is located between the 3 and 6 m contours (above sea level).

The soil is fairly uniform, in the greater part of the area consisting of sand with a grain size of 0.6—0.2 mm which constitutes about 90 % with only 1 % of dredgeable constituents according to *Køie's* analyses (cited from *Weis-Fogh* (1948)), i.e. closely corresponding to drift sand. The soil everywhere displays single grain structure. A typical profile of the Plain shows an upper layer about 20 cm thick consisting of dark, sandy soil containing humus and more or less interwoven with roots. Under this is found a layer of light humus-coloured sand devoid of roots and lowermost a layer of stony yellow sand. The ground water table fluctuates during the year with maximum height in the winter when the lower part of the sampling line may be flooded and minimum in summer, when the water table generally is about 80 cm below the surface.

The vegetation shows certain phases among which must be mentioned the dry *Hieracium pilosella, Gnaphalium arenarium, Polytrichum piliferum* community and the moist *Carex demissa, Hieracium auricula* community with transitional zones with *Jasione montana, Sieglingia decumbens* etc.

On this pasture *Weis-Fogh* (1948) marked out a sampling line 12 m long and with a difference in level between the two end points of 46 cm. On the line 7 stations were erected (I—VII) ranging from the dry *Gnaphalium arenarium* community through the *Agrostis-Sieglingia* to the moist *Carex demissa* community. For detailed description of the line and the Plain see *Weis-Fogh* (l. c.)

For my purposes I first took samples from all seven stations, however, it was found satisfactory to restrict investigations to st. I + II and VI + VII. My two stations may be characterised:

Pl. I + II. Sandy soil with single grain structure, poor and temporarily dry, with only a small root content, the plant cover consisting of *Hieracium pilosella, Polytrichum piliferum, Cladonia spp.*, in addition *Gnaphalium arenarium, Festuca*

ovina, Scleranthus anuus and *Agrostis canina* occur. The vegetation is not completely closed. In the lower part of this station the degree of cover increases without, however, forming a continuous carpet. Also *Jasione montana* and *Trifolium arvense* occur here.

Pl. VI + VIII. Sand of single grain structure with a dense grass carpet, rich in roots and humus. The vegetation consists mainly of *Carex demissa, Sieglingia, Agrostis tenuis, Brunella vulgaris, Hieracium auricula* (especially at the lower end), *Achillea millefolia* and *A. ptarmica* besides some mosses *(Dicranum scoparium, Hylocomium squarrosum* etc.). In contrast with the previous station the vegetation covers the ground entirely forming a vigorous turf, the humus content is high, and during the winter the station is often flooded but never water-logged during the summer. Thus it cannot be classified with the permanently moist localities mentioned later on. However, it is essentially different from Plain I + II.

The fauna of this locality was examined as follows: St. I + II and VI + VII: 20. VII. 1945: 3 and 5 samples respectively, Oct. 1945: 5 samples, Jan. 1946: 5 samples, Nov. 1946: 9 and 5 samples respectively. In July 1947 6 samples were taken from st. VI + VII. All these samples consist of 5 cc soil, the sampling depth being 5 cm. In July 1945 and Oct. 1945 3 samples were taken in each of the localities for the purpose of getting an impression of the vertical distribution of the fauna. These samples were extended to a depth of 25 cm and the whole column separated into 25 small samples each 1 cm high (area 1 sq. cm).

In table 2* the result of the extractions is given on the basis of the primary material of table 2 a*. The species met with (for authors see chapter 11) are arranged in the first column according to decreasing total number (n) and the percentage of the whole material, which each species constitutes of the total number of individuals (st. I + II 21 142, st. VI + VII 25 470) (second column). Besides this the constancy percentage of each species is given in the third column (C. %). This percentage gives an impression of the regularity of the distribution, being the percentage of the total number of samples (each 5 cc) in which the respective species were found.

It may be mentioned here, that the commonly used technique of grouping the species according to the abundancy and constancy (for further discussion see *Kontkanen* (1948)) is not followed here.

For arthropods e.g. *Krogerus* (1931) uses the following principles: Constant, accessory and accidental species are those which occur in more than 50 %, in 25—50 % and in less than 25 % of the samples respectively. Dominant, influent and recedent species constitute 5 % or more, 5—2 % and 2 % or less of the total number of individuals nespectively.

The reason why I have abandoned this way of expressing certain features of distribution is that it is of little value until much more information of this micro-

fauna component has been obtained. It is evident from several of my tables that the numerical values used by *Krogerus* cannot be directly employed. Consequently another grouping must be used, however, I believe that the type of distribution is rather to be compared with that of protozoa, but until investigations have been carried out parallel to those undertaken by me and from other climatic zones a grouping will probably create more confusion than clarity. Instead of this I have preferred to give the different values alone, only excluding all species which constitute less than 1 % (in reality 0.5 % as only integers are operated with). This group is called insignificant species, the term to be understood literally.

A glance at table 2 shows that it is very difficult to establish any grouping of the species met with in the two stations, the total number and the percentages gradually decreasing. According to *Krogerus* (1932) 7 species would be dominants in Plain I + II. Thus his procedure will stress the similarities of different localities instead of being an aid in characterizing them. However, it may be justifiable to regard *Plectus granulosus* and *Aphelenchoides parietinus* as the species which dominate the picture as a whole, in either of the stations (in the table heavy types in the columns for "n" and "%"). Also in other respects the two localities exhibit practically identical faunas in spite of the widely different nature only two exceptions being worthy of mention, *viz.* that *Monhystera vulgaris* seems to be more numerous in st. VI + VII than in st. I + II whilst *Tylencholaimus mirabilis* has practically disappeared in st. VI + VII.

The number of individuals per sq.m in the two stations is given below the total number. Here, too, agreement is found between the stations, the number in both cases amounting to 10 million.

In comparison with other localities this number is rather high, the variation ranging from about 175 000 to 20 million according to the locality.

The weight of the nematodes per sq.m was calculated according to table 1 as 13.5 and 14 g respectively, i.e. identical values. Also in this respect the fauna of the Plain is rather high, the weights in different localities varying from 1 to 20 g per sq.m. These two facts will be discussed in detail in a later chapter, the numbers only being stated to give an impression of the nematode biomass. It may be pointed out that identical numbers per sq.m do not involve identical weights.

The total fauna also comprises a series of insignificant species not specified in the table. With the exception of *Tylencholaimus mirabilis* all the other species would enlarge the table unnecessarily, so they are only mentioned in the text.

The following species were found: *Tylenchus davainei, Rotylenchus robustus, Paraphelenchus pseudoparietinus, Achromadora dubia, Tylenchus filiformis, Mononchus papillatus. Dorylaimus carteri, D. hofmänneri, Tylencholaimus stecki, Cephalobus elongatus, Monhystera agilis, Alaimus primitivus, Aphelenchus sp., Dorylaimus bastiani, D. gracilis, Tylenchorhynchus dubia, Monhystera similis,*

Plectus communis, Panagrolaimus rigidus, Bastiania gracilis, Wilsonema otophorum, Rhabditis monhystera, Mononchus brachyurus, Dorylaimus rhopalocercus (st. VI + VII), *Teratocephalus palustris* (st. VI + VII), *Cephalobus striatus, C. oxyuroides, Aphelenchoides helophilus, Cephalobus nanus* and *Criconema rusticum* (st. I + II).

The discussion of the vertical distribution is postponed until chapter 6.

In this place reference is made to table 2 a, which shows that the seasonal variation of numbers eventually being present is so small that it cannot be demonstrated on the basis of this fairly large material. This contrasts with *Seidenschwarz* (1923) who found a marked maximum during the summer. Probably this is connected with the assumed constantly moist nature of his locality. In most ordinary mineral soils the seasonal variation is believed to be small — as in the Plain. A still more convincing example of the constancy is furnished by a series of samples taken inside one sq.m. in Nørre Fælled in Copenhagen throughout a year. The nematode counts from 6×5 cc were as follows:

IX. 1945: 4725	VIII. 1946: 4848.
X. 1945: 6028	IX. 1946: 5222.
XI. 1945: 3944	X. 1946: 4823.
XII. 1945: 5379	XI. 1946: 6268.
I. 1946: 4639	XII. 1946: 4538.
II. 1946: 5084	II. 1947: 4547.
III. 1946: 4763	V. 1947: 4659.
V. 1946: 5228	VIII. 1947: 4778.
VI. 1946: 3932.	

On comparing these two stations it must be stressed that the moisture relations and the nature of the soil are widely different as was stressed by *Weis-Fogh* (1948) and clearly shown in his figures 15 and 17. Nevertheless the nematode fauna is identical throughout the sampling line. This may be taken as an indication that a characterization of the fauna of different localities mainly on the basis of qualitative differences requires an essentially different composition, as it is a typical feature of nematode distribution that qualitative similarities are common while quantitative differences may be fairly large.

The same fact will be apparent in other localities, thus a type of distribution is found which is similar to that of bacteria and protozoa; most species occur in all types of locality but often with very different abundancy. In microarthropods it is often possible to characterize the fauna of different localities on a qualitative basis alone. A comparison with *Weis-Fogh's* results will illustrate this clearly. In the very same two stations, I and VII, he found the following composition of the fauna of mites and collembola.

	% in Plain	
	I	VII
Folsomia quadrioculata	*25	3
Variatipes quadrangularis	*9	
Tullbergia krausbaueri	*8	
Nanorchestes arboriger	*5.4	
Tectocepheus velatus	*4.2	*17
Isotoma viridis	2.7	
Brachychthonius sellnicki	3	
Brachychthonius berlesei	2.5	
Malaconothrus globiger		*25
Scheloribates laevigatus		*8
Hypogastrura armata		3
Arctoseius bispinatus		3
Oppia clavipectinata		2.5

The list comprises all the dominant and influent species (i. e. species which each constitute 2 % or more of the total fauna). The species marked with an asterisk are "dominants" according to the principles employed by me in the tables (i. e. the most common species, together constituting ca. 50 % of the fauna). It is evident from the list that the fauna of microarthropods is widely different in the two stations, only one dominant *(Tectocepheus velatus)* being common to both of them. This result contrasts very sharply with my table 2. Apparently most nematodes have environmental requirements which are satisfied in almost all localities in contrast with most microarthropods. However, exceptions occur as will be discussed in chapter 5.

2. Shore beach.

Five series of samples were taken on the shore beach of Ebeltoft Vig adjoining the grounds of the Mols Laboratory.

By means of a theodolite a sampling line was established perpendicular to the shore line traversing the different zones of vegetation. The difference in height between the two terminal fix points was 113 cm, the distance between them 29.45 m, the outer point being situated on the shore line. By digging holes in 6 places the water table was found as shown in fig 1 (July 1947). Throughout the line the soil consists of pure sand almost devoid of organic matter and of a homogeneous particle size — except for some irregular layers of coarser sand

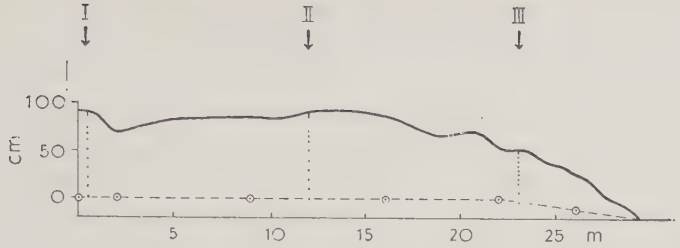

Fig. 1. Transect of the beach. Arrows indicating sampling stations. Full horizontal line: level of sea surface, broken line: ground water table as evidenced by 6 measurements. Sampling depths indicated in the three stations by dots, each representing 5 parallel samples with a total volume of 25 cc.

10—15 cm above the water level at some points on the line. At the time of surveying the largest waves reached the point "26 m".

The vegetation shows a fairly definite zonation. Inland from "0 m" is a uniform area with a rather dense carpet of *Festuca rubra, Corynephorus canescens, Galium verum, Empetrum nigrum, Rhacomitrium sp., Peltigera sp.*, etc.

From "0 m" outwards the following zones may be distinguished:

0—11 m: The vegetation consists mainly of *Festuca rubra, Corynephorus canescens, Carex arenarium,* in the upper part of the line with scattered *Galium verum, Hieracium pilosella* and *Hypochoeris radicata.* From 5 m onwards *Phragmites communis* and *Elymus arenarius* are present in addition.

At about "11 m" the dense vegetation disappears, the dominating species from this point onwards being *Carex arenaria, Elymus* and *Phragmites*, here and there interspersed with *Suaeda maritima.*

From "17 m" onwards only *Elymus, Suaeda, Ammophila arenaria, Agropyron junceum* and *Honkenya peploides* are present. From "25 m" onwards the beach is bare.

A transect of the beach is shown in fig. 1. At the points indicated by vertical arrows 5 parallel samples each of 5 cc sand were taken in each of the depths indicated.

In table 3* the total number of individuals found in the 50 samples from each of the stations, together with the percentage distribution of the species is given. The species marked with an asterisk are marine. As is to be seen from table 2 the fauna of the first station is 1 % marine, that of st. II 11 % and that of the outer station 35 % marine. The most important species are at st. I: *Acrobeles ciliatus, Prismatolaimus dolichurus* and *Achromadora dubia* (together constituting 58 % of the fauna), at st. II: *Prismatolaimus dolichurus, Achromadora dubia* and *Rhabditis sp.* (constituting 60 %) and at st. III: the marine species *Dorylaimopsis punctatus, Achromadora dubia, Prismatolaimus dolichurus, Rhabditis sp.* and *Cephalobus oxyuroides* (constituting 62 %). Apart from the gradual increase in

marine species towards the shore line there is no large difference between the fauna of the single stations, *Prismatolaimus dolichurus* and *Achromadora dubia* as dominants being common to all 3 stations and *Rhabditis sp.* as a dominant species common to st. II and III. If the marine elements of st. III are excluded from consideration *Rhabditis sp.* constitutes 15 % of the total fauna of st. III.

At st. I *Bastiania gracilis* was found as an insignificant species. At st. II the following were found: *Tylenchus sp., Rotylenchus robustus, Cephalobus nanus, Acrobeles demani, Teratocephalus crassidens, Bastiania gracilis* and *Nematoda spp.* At st. III *Tylenchus sp., Dorylaimus centrocercus, Cephalobus nanus* and *Nematoda sp.* were insignificant

Three species deserve special attention. *Mononchus rotundicaudatus* was hitherto only known from the Frisches Haff (among algae) and from the south coast of Sweden (on roots of *Cakile).* The species was described by *Skwarra* (1921) from one juvenile specimen later on *Allgen* (1934) stated that apart from the shape of the tail it does not differ from *M. brachyurus.* I am able to confirm the statement of *Allgen. Choanolaimus psammophilus* is only known from Holland where it is confined to sand dunes according to *De Man* (1884), nor has it been found outside this type of locality by me, not even in samples from inland dunes consisting of pure sand. It is thus rather improbable that the sand itself is the main factor, the major reason for its restricted occurence is probably to be found in some halophilous relation. It feeds on other nematodes as does *Mononchus. Dorylaimus balticus* has only been found "im Küstengrundwasser" at Kiel, thus there is complete agreement as regards the type of locality, as it was only found at st. III.

On account of the special type of vertical distribution to be discussed in a later chapter it is possible to state neither number nor weight of the fauna per sq. m.

Fifteen m above the upper marker point of the sampling line just mentioned two series of samples were taken one below large, dense cushions of *Rhacomitrium sp.* and another in the dense vegetation consisting of *Festuca rubra, Galium verum* etc. The vegetation proper is dense but no litter layer is present.

In table 4* a survey of the fauna of the upper 10 cm of soil is given (Oct. 1945: 10 samples, July 1946: 10 samples).

The richer fauna was found under the moss cover, 2 million individuals per sq. m = 5 g, while under grass cover only 1 million were found, corresponding to 2 g. Also qualitative differences were present between the fauna under moss and under grass cover. In the latter place *Teratocephalus crassidens, Tylencholaimus mirabilis* and *Dorylaimus obtusicaudatus* represent 49 % of the fauna (total 475 000 individuals per sq. m), while under moss cover *Plectus parvus,*

P. cirratus, *Mononchus papillatus* and *M. brachyurus* represent 50 % of the fauna (1 million per sq. m), thus none of the dominating species are common to the two localities.

The following insignificant species were found under grass cover: *Acrobeles ciliatus*, under moss cover: *Plectus longicaudatus*, *Cephalobus persegnis*, *Aphelenchoides parietinus*, *Dorylaimus tritici* and *Monhystera similis*.

It may be concluded, that the upper part of the beach harbours a fauna which is poor in comparison with e. g. the Plain I + II, and that the richer fauna is found below the large, dense moss cushions. Undoubtedly this is due to the protection, which the moss cushions afford against evaporation (see *Overgaard* (1948 b)).

3. The *Corynephorus* slopes.

The type of locality considered under this heading is of a rather uniform appearance and well represented in the grounds of the Mols Laboratory as well as in many places in western Jutland.

The soil of these localities consists of sand of a homogeneous particle size (drift sand). The admixture of organic matter is exceedingly small and mainly consists of fine roots, while humus is almost absent. Podsolization is absent or very weakly developed. Generally the *Corynephorus* slopes occur as isolated spots in heaths with sandy soil. The vegetation is sparse, consisting of rather few species with a low degree of cover corresponding to the extreme exposure of the localities. The slopes are generally located on south facing hill sides and raised well above the water table, the vegetation accordingly consisting of deep-rooted or very drought resistant species.

In the grounds of the Laboratory 4 localities were chosen, all typical in the above respects. For my purposes a subdivision of the localities was undertaken: On a *Corynephorus* slope a certain zonation is generally present. Bordering the locality above we often find a typical *Calluna* heath, then a cluster of *Ononis repens*, below this zone a belt of scattered *Calluna* often occurs and lastly the *Corynephorus* zone proper with a scattered vegetation of *Corynephorus canescens*, *Carex arenaria*, *Hieracium pilosella*, mosses and lichens etc. In this zone often small areas are seen completely devoid of higher vegetation, only with some encrusting lichens covering patches of the soil surface, stones etc.

The following zones were investigated: 1. bare areas in the *Corynephorus* zone, 2. the typical *Corynephorus* zone with a scattered vegetation consisting of *Corynephorus canescens*, *Filago minima*, *Carex arenaria*, *Polytrichum piliferum*, *Cetraria tenuissima*, *Cladonia spp.*, *Rhacomitrium canescens*, *Hieracium pilosella*, *Hypochoeris radicata*, *Teesdalea nudicaulis* etc., 3. tufts of *Calluna vulgaris*, 4. the *Ononis repens* zone, the vegetation of which consists of *O. repens*, *Holchus mollis*, *Agrostis canina*, *Achillea millefolia*, *Knautia arvensis*, *Agrostis tenuis*, *A. stolo-*

nifera, Anthoxanthum odoratum, Agropyron repens and other species forming a high and dense growth, 4. a special area 5 × 15 m on one of the slopes where a beet clamp was placed one of the years about 1936. The area is located in the typical *Corynephorus* zone but shows a distinctly different vegetation consisting of *Corynephorus canescens, Trifolium arvense, Jasione montana, Cerastium semidecandrum, Hieracium pilosella, Hypochoeris radicata, Scleranthus perennis* and other species. The vegetation provides a fairly high degree of cover.

The soil of the *Corynephorus* zone consists of pure sand, under *Calluna* the surface is covered by withered leaves, flowers etc. of *Calluna* forming a layer about 0.5 cm thick. The soil consists of sand with a small amount of organic matter giving a dark colour to the upper cm. In the *Ononis* zone the organic matter content is similar to that of the *Calluna* tufts, but apart from this the soil appears to be somewhat clayey. In the special area where the beet clamp was placed 10 years ago the soil is sandy and contains a little more organic matter causing a darker colour in the upper 5—6 cm of the profile.

In table 5* a synopsis is given of the quantitative and qualitative composition of the fauna in this type of locality. Samples from all 4 stations are incorporated, and the sampling depth was the upper 10 cm of the soil. Samples were taken in January, February, May, June, July and October 1945—47.

In the bare areas the fauna amounts to about 175 000 nematodes per sq. m. (= 1 g), *Dorylaimus obtusicaudatus* and *Tylencholaimus mirabilis* together constituting 75 % of the total number. Insignificant species: *Monhystera vulgaris, Tylenchus filiformis, Criconema rusticum* and *Teratocephalus terrestris* besides an unidentified species of *Mermis* probably associated with *Rhizotrogus* larvae.

The typical *Corynephorus* zone with scattered vegetation seems to harbour a fauna a little richer, the number per sq. m. averaging 375 000 individuals (= 1 g), *Dorylaimus obtusicaudatus, Tylencholaimus mirabilis, Acrobeles ciliatus* and *Cephalobus persegnis* constituting 56 % of the total number. Insignificant species: *Dorylaimus sp., Criconema rusticum, Rhabdolaimus terrestris, Plectus rhizophilus, Monhystera villosa* and the same *Mermis sp.*

Under *Calluna* the fauna per sq. m amounts to 750 000 individuals (= 2 g), *Cephalobus nanus* and *Dorylaimus obtusicaudatus* representing 50 % of the fauna. Insignificant species: *Monhystera villosa, Alaimus primitivus* and *Plectus longicaudatus.*

Under *Ononis* 1.2 million individuals were found per sq. m. (= 2 g), the most important species being *Monhystera vulgaris, Tylencholaimus mirabilis, Dorylaimus obtusicaudatus* and *Tylenchus filiformis* together furnishing 52 % of the population. Insignificant species: *Criconema rusticum, Acrobeles vexilliger, Rhabdolaimus terrestris* and *Mononchus papillatus.*

The locality on hill B, where the beet clamp was placed displays a fauna

distinctly different from that of the typical *Corynephorus* zone in the middle of which it is situated. The number of individuals per sq. m. being 2 million (= 2.5 g). Dominating species is *Acrobeles ciliatus*, constituting 50 % of the fauna. Insignificant species: *Dorylaimus carteri*, *Cephalobus nanus*, *Plectus longicaudatus*, *Diphtherophora communis* and *Alaimus primitivus*.

There is no doubt that this locality deviates in principle from the remaining parts of the *Corynephorus* slopes, and that the increase of the fauna is due to the organic matter introduced ca. 10 years before sampling. This organic matter makes possible a much more intense microbiological activity. Whether part of the nematode fauna was introduced with the beets and the soil adhering to these cannot be decided, in all five localities the fauna is considerably poorer than in the Plain. In a qualitative respect distinct differences are present too. The abundant occurrence of *Dorylaimus obtusicaudatus*, *Tylencholaimus mirabilis* and *Acrobeles ciliatus* deserves special attention.

4. *Calluna* heath, sand.

A large proportion of the grounds belonging to the Mols Laboratory is covered with *Calluna* forming a typical heath. The larger part of this heath is situated on sandy soil, raw humus only occurring on some hills in different parts of the grounds.

In this section only heath on sandy soil is considered. All the areas investigated are highly elevated above the water table and very diversified inclinations are met with from horizontal areas to steep slopes facing all directions. Most of the samples were taken within the area between the permanent marker points 14—15—23—24 (see *Thamdrup* (1948)).

The soil is rather uniform. A typical profile shows the following layers:

0—1 cm: Sand with some organic matter and many fine roots producing a somewhat felted structure.

1—25 cm: greyish to brownish sand, rather sharply demarcated from

25—125 cm: yellowish to reddish sand with some scattered lighter patches and with many stones.

The vegetation mainly consists of *Calluna vulgaris* generally growing in tufts, the interstitial areas being either bare or with a scattered vegetation of *Hieracium pilosella*, *Gnaphalium arenarium*, *Cladonia spp.*, *Polytrichum piliferum*, *Hylocomium parietinum*, *Dicranum scoparium* etc. In the lower areas the *Calluna* is higher and denser and the low vegetation mainly restricted to *Hylocomium parietinum*, *Dicranum scoparium* and *Scleropodium purum*.

In this type of locality a great many samples have been taken at different times of the year (January, February, May, June, July, September and October).

In table 6* the analysis of 40 samples is given. The samples were scattered all over the area mentioned above, this explains the sometimes rather low constancy percentages. In a series of samples taken within some sq. m. the fauna is much more homogeneous. However, in spite of the widely dispersed sampling localities the fauna is very uniform consisting of rather few species and on an average with about 800 000 individuals per sq. m (= 2 g). The dominating species are *Tylencholaimus mirabilis* and *Dorylaimus obtusicaudatus* together constituting 55 % of the fauna with 458 000 individuals per sq. m. Besides the species listed in the table the following have been noted within this type of locality: *Alaimus primitivus, Pharetrolaimus sagittifer, Diphtherophora communis, Tylolaimophorus typicus, Tylencholaimus stecki, Dorylaimus microdorus, D. tritici, Tripyla setifera, Mononchus papillatus, Achromadora dubia, Wilsonema auriculatum, W. otophorum, Rhabdolaimus terrestris, Plectus cirratus, P. rhizophilus, P. longicaudatus, Monhystera villosa, Rhabditis spp., Teratocephalus crassidens, Acrobeles vexilliger, Cephalobus elongatus, C. persegnis, Panagrolaimus rigidus, Tylenchinae spp.* and *Criconema rusticum.*

A closer comparison with the fauna of other Danish *Calluna* heaths could not be made in this connection, however, an attempt at such a comparison was made in the following way. The fauna of a heath plot 2 km south of Studsgaard (western Jutland) was analysed by means of ten samples (June 1946). In table 6 the figures obtained are given. *Cephalobus nanus* and *Acrobeles ciliatus* constitute 50 % of the fauna (643 000 per sq. m) while on Mols they were important although not dominant (together 16 % = 133 000 per sq. m). It is evident that there is quite a close resemblance, most species being common to both areas. In a quantitative respect too the divergencies are small: 1.3 million per sq. m (= 1.7 g).

From the large heath area between Söby and Högild (ca. 10 km S. of Herning) 8 larger samples were taken in June 1946, 500 individuals taken at random were identified and the proportion made up by the 8 commonest species was calculated. The result of this analysis is shown in fig. 2, where the two last columns indicate the percentage distribution of the same species in the samples from Mols and Studsgaard respectively.

Perhaps this procedure gives the best impression of the slight degree of qualitative variation. The 8 species mentioned constitute together from 62—96 % of the total fauna of the dry *Calluna* heath on sandy soil in the 10 series of samples from different parts of Jutland.

A comparison with the previous localities shows that the fauna of the typical heath on sandy soil is not essentially richer than the fauna found under isolated *Calluna* tufts on the *Corynephorus* slopes. No characteristic species are found to be typical of heaths. In comparison with the Plain the fauna is poor.

Fig. 2. The percentages constituted by the eight commonest species in eight samples from the heath south of Herning; 100 % = 500 specimens. In the two last columns the importance of the same species in the samples of table 6 are shown. The species are as follows: 1.*Cephalobus nanus*, 2. *Prismatolaimus dolichurus*, 3. *Dorylaimus obtusicaudatus*, 4. *Monhystera vulgaris*, 5. *Tylencholaimus mirabilis*, 6. *Tylenchus filiformis*, 7. *Acrobeles ciliatus*, 8. *Cephalobus persegnis*.

5. Grass fields, Mols.

In a moraine landscape like that which occurs around Agri in Mols and in which the grounds belonging to the Mols Laboratory are situated, every type of exposure is to be met with combined with different levels and irregular dispersal of soil types.

In order to elucidate the influence of these factors upon the qualitative and quantitative composition of the fauna a sampling line was marked out near the road from Strandkjær to Agri. In fig. 3 a diagram of the line is shown. The soil of the 5 different stations may be characterized as follows:

I. Soil brown, clayey sand mull with single grain structure, during the winter rather moist, during the summer exhibiting optimum water relations for plant growth, and never subject to drought. The vegetation mainly consists of excellent

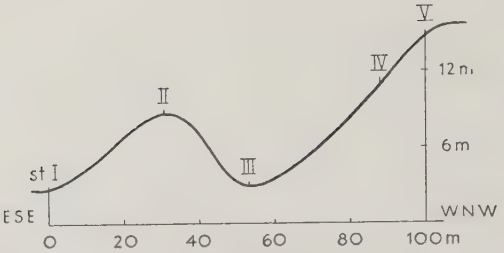

Fig. 3. Transect of the sampling line in the grass fields in Mols.

food grasses: *Anthoxanthum odoratum, Phleum pratensis, Dactylis glomerata, Lolium perenne, Trifolium repens* and others forming a dense cover.

II. On the top of the hill the soil is decidedly poorer, humus content small, the soil consisting of pure sand with a small clay fraction. The vegetation is very open and shows signs of soil drought, *Hieracium pilosella, Jasione montana, Geranium pusillum* besides some mosses (especially *Ceratodon purpureus)* are important.

III. Soil sandy mull, not clayey as in st. I. The vegetation takes up an intermediate position between I and II, *Phleum pratense, Poa pratensis, Hieracium pilosella* and *Jasione montana* are absent and in contrast with I and II *Trifolium pratense* is common, however, the growth is somewhat impoverished. A little moss is also present.

IV. The soil consists of sand, the upper 5 cm containing some humus which gives the layer a brownish-black colour which at this depth gradually changes into yellow-brown sand. In the upper 15 cm roots are present, the upper 5 cm containing a very dense net of vigorous roots. The vegetation mainly consists of *Agrostis tenuis, Dactylis glomerata, Festuca rubra, Hieracium pilosella, Jasione montana, Achillea millefolia, Euphrasia sp., Ononis repens, Cladonia spp., Polytrichum piliferum* and other mosses.

V. This locality is very typical as the soil and vegetation picture exhibited here is met with abundantly in Mols and many places in western Jutland. It is found where old grass areas on sandy soils have been abandoned and let grow wild. Gradually the cultivated grasses disappear, grasses with little agricultural value appear, and after some years single tufts of *Calluna* settle. Later the *Calluna* cover will grow denser and a typical heath will result in some years.

The soil at st. V consists of very poor, sharp sand, the upper 2 cm containing a rather loose root system. The colour does not deviate much from the yellowish-brown subsoil. The vegetation consists of *Hieracium pilosella, Jasione montana, Ononis repens, Gnaphalium arenarium, Achillea millefolia, Calluna vulgaris* (as scattered tufts), *Cerastium semidecandrum, Polygala vulgare* besides *Polytrichum piliferum* and *Cladonia spp.*

At each of the stations 10 samples were taken (depth 0—5 cm). In table 7* an analysis of the fauna is given. From this survey it is easily seen that the great differences in regard to soil and vegetation are correlated with quantitative as well as qualitative differences.

Station I exhibits an extremely rich fauna amounting to 17 million per sq. m. (= 10.5 g) and with *Ditylenchus intermedius* (42 % = 7.1 million per sq. m), as a dominating species. In addition *Cephalobus persegnis* and *C. oxyuroides* are important (together constituting 39 % = 6.5 million per sq. m).

As is to be expected from the above description st. II shows the greatest resemblance to st. I, however, the fauna is poorer quantitatively (6 million individuals corresponding to 8.5 g per sq. m.), the dominating species being *Cephalobus persegnis, Plectus granulosus* and *Tylenchorhynchus dubia* (together 54 % = 3.2 million per sq. m.).

Some resemblances are found between st. II and IV the numbers and weights respectively being 4 and 5 million individuals and 6 and 10 g. Dominating species at st. II are: *Plectus granulosus* and *P. cirratus* (together 57 % = 2.3 million per sq. m.), at st. IV: *Plectus granulosus* and *Dorylaimus carteri* while *Tylenchorhynchus dubia* in st. IV is still present in practically the same number as in st. III.

Just at st. I takes up an isolated position in comparison with the remaining stations, so also st. V deviates much from I—IV. The number of individuals has decreased to 2 million per sq. m. while the weight is 8 g. The dominating species are *Tylencholaimus mirabilis, Dorylaimus obtusicaudatus* and *Acrobeles ciliatus* (together 70 % = 1.7 million per sq. m.), all of them species unimportant or even lacking in st. I, while they are found as dominating species in many *Calluna* heaths, *Corynephorus* slopes and other poor localities (see these two sections).

The following insignificant species were met with. St. I: *Monhystera vulgaris, Acrobeles vexilliger, Prismatolaimus dolichurus, Alaimus primitivus, Tylenchus sp., Cephalobus striatus, Aphelenchus avenae, Bastiania gracilis, Dorylaimus tenuicollis, D. tritici, Plectus geophilus, Diphtherophora communis, Rhabditis monhystera* and *Rh. longicaudata.* St. II: *Plectus parvus, Tylencholaimus mirabilis, Paraphelenchus pseudoparietinus, Prismatolaimus dolichurus, Cephalobus striatus, C. longicaudatus, Tylenchus sp., Aphelenchus avenae, Bastiania gracilis, Dorylaimus monhystera* and *Wilsonema tentaculatum.* St. III: *Dorylaimus tritici, Diphtherophora communis, Rhabditis monhystera, Rhabdolaimus terrestris, Bastiania gracilis, Prismatolaimus dolichurus, Rhabditis longicaudatus, Teratocephalus crassidens* and *Wilsonema otophorum.* St. IV: *Dorylaimus tritici* and *D. sp.* St. V: *Plectus longicaudatus, Aphelenchus avenae, Tylenchus sp.* and *Longidorus sp.* In table 7 the remaining insignificant species from all stations have been mentioned where this was possible without waste of space.

At this point it may be mentioned that *Wilsonema tentaculatum* is considered

to be associated with bark beetles by *Fuchs* (1930). I am not able to go into details of this question, however, in st. II it lives, of course, completely independant of these insects as is also the case in some other localities where I have found the species in soil.

6. Other grass fields.

In the preceding sections different types of grass fields have been analysed. Plain I harbouring about 10 million nematodes per sq. m. may serve as an example of a pasture of low agricultural value: the vegetation in the lower section of the sampling line is almost closed, but the agricultural value of the species forming the plant cover is small. Among the localities analysed in table 7 the stations II, III and IV are somewhat reminiscent of Plain I although the nematode fauna is poorer while the agricultural value of the localities is still low. St. V is decidedly poorer both as regards agricultural value and nematode fauna. In st. I a locality of high agricultural value and a rich nematode fauna occurs.

In the vicinity of Studsgaard some grass fields were examined all belonging to the same type: rather dry to very dry soil and with a low degree of vegetational cover which mainly consisted of plants with small agricultural value. The number of nematodes found in these localities ranged from 8 to 1 million per sq. m., the most important species being *Cephalobus persegnis, C. nanus, Rotylenchus robustus, Prismatolaimus dolichurus, Monhystera vulgaris, Dorylaimus obtusicaudatus, D. carteri, Tylenchus filiformis, Teratocephalus terrestris* and *Plectus granulosus.*

A much richer fauna was found in luxuriant grass fields located on soil of about optimum moisture status. Two analyses are given in table 8*, each comprising 10 samples taken in August 1946.

The field at Studsgaard is a typical ley with agriculturally selected plants *(Lolium perenne, L. multiflorum, Trifolium pratense* etc.) while the locality at Herning is a natural pasture with *Anthoxanthum odoratum, Agrostis stolonifera, Holchus lanatus, Festuca rubra, Lolium perenne* etc.). The growth is in both cases luxuriant with a high degree of cover.

The fauna is — as will be seen from the table — amazingly similar in the two localities. At Studsgaard the total fauna amounts to 20 million per sq. m. (18 g) the two dominant species (at Studsgaard *Tylenchorhynchus dubia* and *Plectus granulosus*, at Herning *Plectus granulosus* and *Cephalobus persegnis)* constituting 64 and 67 % resp. of the total fauna with 13 and 11 million individuals per sq. m. respectively).

In comparison with other localities the total numbers are still larger than in st. I of table 7, but of the same order of magnitude. As to the species composition a rather close agreement with the fauna of st. III of table 7 is found, the three species mentioned above are the most important in all 3 localities. At Studsgaard they constitute 74 % = 15 million per sq. m., at Herning 78 % = 15 million and at Strandkjær 54 % = 3 million per sq. m.

7. Cultivated land.

At the State Experiment Station of Studsgaard (Jutland) 2 series of samples were taken (35 samples each). The plots investigated are parts of a fertilising experiment which was started in 1917 comprising 8 plots; from 1927 the experiments were carried on in 4 plots (B 1—4). A full account of the experiments is given by *Hansen* (1948).

The following experimental layout was employed: The four plots are located on light sand soil with sand subsoil and with the following crop rotation: 1. rye, 2. turnip or potato, 3. oats and 4. clover-grass or lupine. In 9 phases of the experiment the following nutrients were administered: 1. untreated, 2. 1/2 stable manure, 3. 1 stable manure, 4. 1 1/2 stable manure, 5. 1/2 unit of fertilizer, 6. 1 fertilizer, 7. 1 1/2 fertilizer, 8. 1/2 stable manure + 1/2 fertilizer and 9. 1 stable manure + 1/2 fertilizer. In the remaining 8 phases 1 stable manure was administered and in addition varying quantities of different fertilizers.

1 unit of stable manure was defined as follows:

for rye	6 t liquid manure.
for turnip or potatoes	27 t stable manure + 6 t liquid manure.
for oats	9 t stable manure + 0 t liquid manure.
for clover-grass	0 t stable manure + 0 t liquid manure.

Expressed as kg N per ha per 1 manure or fertilizer the administration was as follows:

In case of stable manure: rye 16.0, potatoes 157.8, oats 45.1 and lupines 0. Mean: 54.8 per year of the crop rotation.

In the case of fertilizer: rye 19.6, potatoes 160.0, oats 47.0 and lupines 0. Mean: 56.7 kg N.

Among the phases the following were examined in respect of nematodes: 1. untreated, 2. 1/2 stable manure, 3. 1 stable manure, 4. 1 1/2 stable manure, 5. 1/2 fertilizer, 6. 1 fertilizer, 7. 1 1/2 fertilizer.

It was found that the differences of the total fauna in the respective phases were only small. The total number in 1000 of nematodes per sq. m was as follows:

	rye field	turnip field
1. untreated	1800 ± 180	1100 ± 71
2. 1/2 manure	2200 ± 132	1300 ± 99
3. 1 manure	2200 ± 144	900 ± 63
4. 1 1/2 manure	3200 ± 158	1100 ± 110
5. 1/2 fertiliser	2200 ± 126	1000 ± 113
6. 1 fertiliser	2800 ± 132	900 ± 100
7. 1 1/2 fertiliser	2400 ± 120	1300 ± 122

The fauna of the single phases is not very different apart from a certain tendency towards a decrease of number in the unfertilised plots in the rye field. At all events the size of the total fauna is small, not exceeding that of several localities with an open vegetation, and much less than that of dense grass fields or even the Plain. The average of the total material amounts to 2.5 million per sq. m. corresponding to 3 g in the rye field. In the turnip field the numbers from the different plots were similar too but the total number distinctly lower, corresponding to ca. 1 million per sq. m. (0.7 g).

As regards the species composition the following results were obtained (table 9*): In the rye field *Prismatolaimus dolichurus, Cephalobus nanus* and *Rhabditis monhystera* constitute 48 % of the fauna (1.2 million = 0.3 g). In the turnip field *Prismatolaimus dolichurus, Monhystera vulgaris* and *Cephalobus persegnis* constitute 51 % of the fauna (500 000 = 0.1 g), the qualitative differences between the two phases thus being small.

The following insignificant species were found in the rye field: *Acrobeles vexilliger, Dorylaimus tritici, Acrobeles ciliatus, Panagrolaimus rigidus, Tylolaimophorus typicus, Ethmolaimus pratensis, Wilsonema otophorum, Achromadora dubia, Mononchus papillatus, Dorylaimus limnophilus, Criconema rusticum, Diphtherophora communis, Alaimus primitivus, Dorylaimus micoletzkyi, Dorylaimus sp., Plectus longicaudatus, Pharethrolaimus sagittifer, Dorylaimus bryophilus, Tylenchus sp., Mononchus brachyurus, Teratocephalus terrestris, Dorylaimus bastiani, D. ettersbergensis, Rhabditis filiformis* and *Tylencholaimus mirabilis.* In the turnip field the following occurred: *Dorylaimus tritici, Paraphelenchus pseudoparietinus, Acrobeles ciliatus, Plectus parvus, Mononchus papillatus, Criconema rusticum* and *Plectus longicaudatus.* Thus the fauna is poor consisting of species occuring abundantly in most localities.

8. Meadow, sand.

This type of biotope is rather uncommon. Generally the humus content in the moist areas is so high that they must be termed organic soils. At Rind Aa (Bærslund, 8 km S. of Herning) I have examined a locality which belongs to the mineral type (June 1946). The soil consists of pure sand intermixed with some ocherous sediments forming small dredgeable floccules. Located 150 cm from the border of the rivulet the soil is permanently moist. The vegetation is luxuriant and completely covers the surface. The most important plants are: *Deschampsia caespitosa, Poa pratensis, Holchus lanatus, Alopecurus pratensis, Lychnis flos cuculi, Ranunculus acer, Cardamine pratensis* and *Myosotis hispida.*

In table 10* a survey of the fauna is given. In spite of the high degree of cover of the vegetation, the fauna is much poorer than in the localities analysed in table 8. Per sq. m. only about 1.5 million of nematodes are found corresponding to a weight of 1.3 g. *Plectus cirratus* and *Aphelenchoides parietinus* together constitute 51 %

of the fauna. In comparison with the localities hitherto discussed the species composition of the fauna is highly aberrant as a series of typical freshwater species occur: *Monhystera filiformis, Dorylaimus limnophilus, D. stagnalis, D. centrocercus, D. brigdammensis* and *Mononchus macrostoma* do not occur in the previously analysed localities while they here constitute 40 % of the total number, *Monhystera filiformis* even being of the same numerical importance as *Aphelenchoides parietinus*. In the following tables the typical freshwater species are marked with an asterisk.

Besides the species mentioned in the table, the following are found in insignificant numbers: *Paraphelenchus pseudoparietinus, Dorylaimus longicaudatus, Cyatholaimus intermedius, Plectus granulosus, Rhabdolaimus terrestris* and *Diphtherophora communis.*

This locality is discussed again in view of the water status, which explains the occurrence of the new fauna component met with here (p. 61).

9. Meadow, mull.

The area forms a direct northern continuation of the Plain in the grounds of the Mols Laboratory. The locality is surrounded by trees (especially alder and ash). Apart from hay-making it is uncultivated.

The soil of the upper 70 cm is dark and very rich in humus, below this horizon grey sand is met with. The upper 20 cm. consists of loose mull rich in humus and with many roots. In contrast with the sandy meadow (table 10) and the bog soil of the western part of the Plain to be discussed later on (p. 44) a typical crumby structure is present. In the lower horizons the mull is replaced by a typical bog soil corresponding to that of the Plain. The locality is never flooded and never dries up during the summer.

The vegetation is tall and luxuriant but not very dense, consisting of *Deschampsia caespitosa, Festuca rubra, F. elatior, Poa nemoralis, P. pratensis, Holchus lanatus, Bromus mollis, Alopecurus pratensis, Carex stolonifera, Cerastium caespitosum, Stellaria graminea, S. media, Lychnis flos cuculi, Rumex acetosa, Ranunculus acer, Caltha palustris, Cardamine pratensis, Filipendula ulmaria, Potentilla erecta, Geum rivale Plantago lanceolata, Galium palustre, Myosotis hispida, Trifolium pratense, Rhinanthus major* and *Brunella vulgaris*. 10 samples were taken in October 1945 and 10 in July 1947.

In table 11* a survey of the fauna is given. As will be seen only 1.2 million nematodes are found per sq. m. corresponding to 2.5 g. On the whole conditions resemble strikingly those of the bog soil of the Plain both as regards the density and the species composition of the fauna (see table 16).

The dominating species are *Aphelenchoides parietinus, Monhystera filiformis, Dorylaimus longicaudatus* and *Plectus cirratus* which together constitute 53 % of

the fauna. Nearly all species are common to the bog soil and this mull locality, and the freshwater group constitutes ca. 40 % of the fauna in either of them. In comparison with the Plain the fauna is poor, and it consists to a large extent of species which do not occur there, only *Aphelenchoides parietinus* being common to both as a dominant.

Insignificant species: *Alaimus primitivus, A. dolichurus, Bastiania gracilis, Prismatolaimus dolichurus, P. intermedius, Plectus granulosus, Wilsonema otophorum* and *Tylenchorhynchus intermedius.*

In this locality *Weis-Fogh* found the mites *Platynothrus peltifer* and *Malaconothrus globiger* to be typical, i. e. the fauna of microarthropods is similar to that of Plain VII. In the case of nematodes the fauna is essentially different from that of Plain VII, as the freshwater species do not occur in this latter place.

10. Grass fields, light clay.

The Nørre Fælled in Copenhagen was chosen as a representative of this type. The soil consists of sand with a considerable dredgeable fraction. The clay is, however, not so prominent as to cause a typical sticky consistency of the soil.

The whole area is densely grass grown, the vegetation mainly consisting of *Dactylis glomerata* and *Lolium perenne.*

The locality was investigated several times. The samples of table 12 were taken as follows: May 1945: 5, October 1945: 5, February 1946: 5, August 1946: 5.

In table 12* a survey of the fauna is given (three first columns). The total fauna amounts to 8.3 million individuals per sq. m. corresponding to a weight of 6.5 g. The dominating species are: *Tylenchorhynchus dubia, Aphelenchoides parietinus, Prismatolaimus dolichurus* and *Monhystera vulgaris* together constituting 52 % of the fauna.

Besides the species mentioned in the table the following insignificant species were met with: *Alaimus primitivus, Pharethrolaimus sagittifer, Dorylaimus carteri, D. tritici, Tripyla setifera, Ethmolaimus pratensis, Achromadora dubia, Plectus geophilus, Rhabditis filiformis, Acrobeles demani, Macrolaimus crucis* and *Paraphelenchus pseudoparietinus.*

The fauna of this area does not deviate essentially from that of several other grass fields on sand soil. All the dominants are common on the Plain. The great abundance of *Tylenchorhynchus dubia* seems to be correlated with the dense vegetation. In dense grass fields the number of root sucking *Tylenchinae* will often increase considerably, thus two species *(T. intermedius* and *T. dubia)* are dominants in the grass fields of table 7. *Aphelenchoides parietinus, Tylenchus filiformis, T. davainei* and *Rotylenchus robustus* may also be numerous in the absence of a dense grass cover.

11. Grass fields, heavy clay soil.

Near the coast of the Lillebelt NW of Assens some fields are present just inside the steep slopes where a very heavy clay prevails. In summer the surface in open areas forms a very hard crust. Under dense grass cover the crust is much reduced.

In a ley with a high degree of cover a sample series was taken in July 1943. The vegetation consisted of *Lolium perenne, L. multiflorum, Trifolium pratense, Veronica spp. Cichorium Intybus* and others.

The fauna amounted to 12.1 million per. sq.m. corresponding to 11.5 g (table 12*).

The dominating species are *Monhystera vulgaris, Plectus granulosus, Aphelenchoides parietinus* and *Tylenchus intermedius* together constituting 50 % of the fauna.

Insignificant species: *Achromadora dubia, Rhabdolaimus terrestris, Monhystera villosa, Paraphelenchus pseudoparietinus, Acrobeles emarginatus* and *Nematoda spp.*

A comparison of the two last localities with several of the preceding representatives of sandy soil shows that the differences (both qualitative and quantitative) between comparable localities on very different soils are indeed, rather small. Thus in the heavy clay soil *Monhystera vulgaris, Plectus granulosus* and *Aphelenchoides parietinus* together constitute 41 % of the total number, in Plain I + II (table 2) the corresponding percentage is 47.

The total number and weight of the fauna in the two localities are 12.1 million = 11.5 g and 10 million = 14 g respectively.

II. ORGANIC SOILS

A more detailed classification of the organic soils is rather difficult on account of the extreme type of water status. The only procedure which I have found suitable for my purpose is to distinguish between two main groups namely the raw humus which is found in several localities, e. g. in the *Calluna* heaths and conifer plantations and the peat which is characterized by its permanently moist condition. A third group may be distinguished to comprise a special bog soil to be found in low areas (especially if they are flooded during the winter). A sharp limit between the two latter groups cannot be maintained, even if some descriptive differences can often be found. In typical cases they may be distinguished by structure, consistency and colour: Peat often consists of fairly intact plant remains of spongy consistency and brownish colour, while the bog soil generally consists of highly decomposed plant matter of a sticky, compact consistency and a dark brown to black colour (in extreme cases showing gleization). In the following this subdivision will be used.

a. RAW HUMUS

The only way of classifying this soil type is in respect of its origin. Here the fauna of four different types is analysed.

1. *Calluna* raw humus.

A typical representative of this type is found in the *Calluna* heath bordering the Högildgaard Plantation S. of Studsgaard.

The area is fairly level with a slight inclination towards the North. The soil profile is typical:

0—25 cm: Dense brownish raw humus with many roots of *Calluna* and *Empetrum*,
25—45 cm: grey, podsolized sand sharply demarcated from
45—60 cm: brown or reddish brown hardpan,
60— cm: red to yellow sand with numerous stones.

The vegetation consists of *Calluna* in large tufts. Under and among the tufts a vegetation is found consisting of *Empetrum*, *Vaccinium Vitis-idaea*, *Arctostaphylos Uva-ursi* and a little *Arnica montana*. Among the mosses *Dicranum scoparium*, *Hylocomium parietinum*, *Stereodon cupressiformis* and *Scleropodium purum* dominate. In addition *Cladonia spp.*, *Peltigera spp.* and *Cetraria islandica* are found.

The fauna of this locality is analysed in the three first columns of table 13* (June 1946: 10 samples, December 1947: 10 samples). As will be seen the total number of nematodes per sq. m. is fairly small in comparison with several mineral soils only amounting to 2.4 million corresponding to 2.4 g. The most important species are *Dorylaimus carteri*, *Tylenchus davainei* and *Plectus cirratus* together constituting 47 % of the fauna.

In comparison with *Calluna* heaths on sand the fauna seems to be somewhat richer (see table 6) the total numbers in this type of locality being usually about 1 million. As to the qualitative composition most species are common to the two types of locality even if their percentage distribution seems to be somewhat different.

Some interesting differences may, however, be pointed out: *Tylencholaimus mirabilis* and *Acrobeles ciliatus* are very typical and often very numerous species in sandy soil while they are rarely found in raw humus. On the other hand *Bunonema reticulatum* (as well as other species of *Bunonema)* is practically never found outside raw humus and moss cushions where it may be numerous in some localities. In one case I have found more than 100 individuals per 5 cc raw humus in several parallel samples. *Acrobeles vexilliger* may be found both in raw humus and in mineral soils, but it is decidedly more numerous in the former type.

Besides the species mentioned in the table the following insignificant species were found: *Tylolaimophorus typicus*, *Dorylaimus regius*, *D. tritici*, *Mononchus*

papillatus, Achromadora dubia, Wilsonema auriculatum, Plectus granulosus, P. rhizophilus, Monhystera villosa, Rhabditis monhystera, Teratocephalus terrestris, T. crassidens, Cephalobus persegnis, C. elongatus, Bunonema richtersi and *Rotylenchus robustus.*

2. Vaccinium raw humus.

Near the eastern outskirts of Tinnet Krat S. of Nr. Snede (Jutland) a locality was chosen where this type of raw humus occurred typically. The locality is situated beside a fence facing the North, and is not covered by the surrounding spruce *(Picea Abies)*, although the locality is overshadowed at some inclinations of the sun.

The profile is:

0—8 cm: Brown raw humus, superficially (1 cm) rather loose, dense below with many coarse and fine roots giving the layer a felted consistency.

8—40 cm: Leached sand somewhat darker above and below, grey in the middle.

40—53 cm: brown, below brownish black hardpan.

53— cm: yellowish sand with stones.

The vegetation consists of *Vaccinium Myrtillus*, among which single individuals of *Trientalis europaea* and *Majanthemum bifolium* and *Peltigera sp.* are found.

In table 13* (three last columns) the fauna has been analysed (June 1945). Per sq. m. the fauna amounts to 2.7 million individuals corresponding to 2.2 g. The dominating species are *Cephalobus nanus, Plectus cirratus, Dorylaimus carteri* and *Aphelenchoides parietinus* together constituting 50 % of the fauna.

A comparison with the preceding locality shows that two of the dominating species are common to both. On the whole the species composition displays close affinities to this locality. *Bunonema reticulatum* as well as *Acrobeles vexilliger* are common here.

Insignificant species: *Mononchus papillatus, Diphtherophora communis, Wilsonema auriculatum, Plectus rhizophilus, Teratocephalus terrestris, T. crassidens, Rotylenchus robustus, Tylenchorhynchus dubia* and *Criconema rusticum.*

3. Spruce raw humus.

This type of raw humus occurs abundantly in the conifer plantations. As an example a station in the central part of Grib forest (Sealand) was chosen. The locality may be compared directly to locality 8 of *Bornebusch* (1930) being located in the same area. The samples were taken under old spruces where the soil was covered by a thin layer of moss, especially *Stereodon cupressiformis.*

The following profile was obtained:

0—2 cm: a thin layer of moss growing on a 2 cm thick layer of needles.
2—10 cm: brownish black raw humus.
10—25 cm: grey leached sand.
25—28 cm: loose and fragmented hardpan.
28— cm: sand, above brown and with some cementing substance gradually becoming reddish and yellowish downwards.

The fauna of this locality is analysed in table 14* (3 first columns) September 1946. The number of nematodes is small, only amounting to 1.7 million per sq. m. corresponding to 4.5 g. The dominating species are *Dorylaimus obtusicaudatus*, *Acrobeles vexilliger* and *Cephalobus nanus* which together constitute 57 % of the fauna.

It may be pointed out that *D. obtusicaudatus* and *C. nanus* are rarely found as dominating species. In the localities hitherto mentioned this was only the case on the beach under grass cover (table 4), in some of the series from the *Corynephorus* slopes (table 5), in the *Calluna* heath on sand (table 6) and in st. V among the grass fields of table 7, all poor localities as regards plants as well as nematodes. On the whole one gets a distinct impression that these two species attain their greatest relative abundancy where conditions are most adverse to the nematode fauna. They may be regarded as species especially resistant towards drought.

A comparison with the preceding table shows that most species from the spruce raw humus also occur in *Calluna* and *Vaccinium* raw humus.

Insignificant species: *Diphtherophora communis*, *Tylolaimophorus typicus*, *Tripyla setifera*, *Monhystera villosa*. *Macrolaimus crucis* and *Procriconema (straeleni?)*

4. Fern raw humus.

This fairly rare type of raw humus was examined at a station in the grounds of the Mols Laboratory. In the western part of the area bordering the Plain, an oak shrub with a very dense growth of *Pteridium aquilinum* is situated. Here a typical fern raw humus is formed which may be 20 cm thick.

A survey of the fauna is given in table 14* (3 last columns) Oct. 1945: 5 samples, July 1947: 5 samples. The dominating species are *Aphelenchoides parietinus*, *Dorylaimus carteri* and *Plectus rhizophilus* together constituting 56 % of the total fauna which amounts to only 1.2 million per sq. m. corresponding to 1.5 g.

Most species occurring are identical with those from the other types of raw humus, however, it may be mentioned that *Bunonema spp.* did not occur.

Insignificant species: *Wilsonema auriculatum*, *Plectus parvus*, *Nematoda sp.*, *Plectus longicaudatus*, *Ecphyadophora tenuissima*, *Plectus granulosus*, *Cephalobus persegnis*, *Criconema (de-mani?)*, *Achromadora dubia* and *Tylenchus filiformis*.

b. PEAT

This type of organic soils was investigated from 5 different places, and everywhere the same fundamental features appeared. Among the localities two were selected as examples.

1. Heath moor.

The locality is situated at the northern boundary of Høgildgaard Plantation 2 km S. of Studsgaard, where a low area intersected by ditches lies between the plantation and the cultivated fields.

The soil consists of rather compact peat extending to a depth of generally 1.5 m under which sand is present.

The vegetation is fairly open and tufted and of a heterogeneous composition. In some places *Narthecium ossifragum* is dominant, while in others *Molinia coerulea, Deschampsia caespitosa, Nardus strictus, Festuca ovina, Eriophorum vaginatum, Scirpus germanicus* and *Juncus squarrosus* are the most important species. Scattered all over the area *Calluna, Erica, Vaccinium Vitis-idaea* and *Orchis maculatus* occur. In June 1946 10 samples were taken, in June 1947: 10. (table 15*).

Dominating nematodes are *Plectus cirratus, Dorylaimus stagnalis* and *Tylenchus filiformis* together constituting 51 %. The fauna is poor, only amounting to 327 000 per sq. m. (= 1 g).

Insignificant species: *Tylolaimophorus typicus, Actinolaimus macrolaimus, Odontolaimus chlorurus, Achromadora dubia, Aphanolaimus attentus, Wilsonema otophorum, Plectus longicaudatus* and *Monhystera similis.*

When compared with other localities the resemblance to the permanently moist mineral soils is evident. The new faunal element appearing in the sandy meadow (table 10) and in the mull meadow (table 11) also occurs here, *viz. Dorylaimus stagnalis, D. longicaudatus, D. centrocercus, D. rhopalocercus, D. brigdammensis, D. limnophilus, Teratocephalus palustris, Mononchus macrostoma, Monhystera filiformis* and some species belonging to the same group but not recorded in the previous localities: *Ironus ignavus, Chromadora ratzeburgensis* and *Trilobus allophysis.* Together this group constitutes 50 % of the fauna. The remaining 50 % of the fauna consists of species of general occurrence in mineral as well as organic soils.

2. High moor.

As a typical locality the Knudmose outside Herning was chosen. The peat extends to a depth of about 2 m. The colour is brown to black and the consistency somewhat spongy with numerous compressed plant remains.

The vegetation is poor, mostly consisting of *Calluna, Erica, Arctostaphylos Uva-ursi, Vaccinium Vitis-idaea* besides a little *Andromeda polifolia* and some

tufts of *Molinia coerulea, Nardus strictus* and *Deschampsia caespitosa.* 20 samples were taken in June 1946.

Dominating species: *Prismatolaimus dolichurus, Plectus cirratus, Monhystera filiformis, Plectus parvus* and *Dorylaimus longicaudatus* together constituting 49 % of the fauna, which is poor, although richer than in the preceding locality. The total fauna averages 770 000 per sq. m corresponding to 1.5 g (see table 15*).

As regards the species composition the locality is reminiscent of the heath moor although some of the typical terricolous species are more abundant and some of the freshwater species have disappeared.

Insignificiant species: *Wilsonema otophorum, Plectus longicaudatus, Pl. granulosus, Cephalobus manus, C. persegnis, Achromadora dubia* and *Diplogaster fictor.*

c. BOG SOIL

As a representative of this category the lower areas of the Plain were investigated. As stated above (p. 20) the greater part of the Plain consists of sand. However in the western and northern areas conditions are different. Here some depressions of the original surface are present where the sand is covered by a 50—70 cm thick layer of heavy, sticky and very compact humus intermixed with roots and with no definite structure. The soil is permanently moist and during the winter often flooded.

The vegetation is fairly dense and consists of hygrophilous species among which may be mentioned: *Carex demissa, C. stolonifera, Poa pratensis, Ranunculus acer, Cardamine pratensis, Myosotis hispida* besides some mosses. The following samples were taken: July 1945: 5, October 1945: 5, January 1946: 10 and November 1946: 5.

The fauna is rather poor (table 16*), amounting to 1.5 million per sq. m. corresponding to 3.1 g. *Rotylenchus robustus, Dorylaimus longicaudatus, D. centrocercus* and *Monhystera filiformis* are dominants and constitute 50 % of the fauna.

A comparison with the mull meadow (table 11) reveals a very close resemblance with regard to species composition and a comparison with the sandy meadow (table 10) shows many species in common. The 6 species mentioned p. 37 which constitute 40 % of the fauna in the sandy meadow and which do not occur in more dry localities constitute 27 % of the fauna here. In the bog soil the group has been augmented by *Dorylaimus longicaudatus* while *D. stagnalis* does not occur.

Besides the species mentioned in the table the following insignificant species were found: *Rhabdolaimus terrestris, Mononchus papillatus, Tylenchus davainei, Prismatolaimus intermedius, Rhabditis monhystera, Panagrolaimus rigidus* and *Mononchus macrostoma.*

5. THE GENERAL DISTRIBUTION OF THE FAUNA

The general distribution of the fauna cannot be discussed without pointing out certain features pertaining to the special biological adaptations of the nematodes and to the technique of obtaining a representative sample of the fauna in the various localities.

Firstly the fact must be stressed that most nematodes regularly occurring in the soil possess the ability to survive frequent desiccations even of long duration. This power can be compared to that of many protozoa.

When nematodes are in the desiccated state their potentialities for passive dispersal with soil, dust etc. are practically unlimited (see e. g. *Gislén* (1948)) and in addition they are very resistant towards extreme physical factors. Thus ca. 75 % of the nematodes of a soil sample would survive 8 days of storage at room temperature + 15 days at ÷ 5° C +6 days in a Berlese apparatus at ca. 40° C. *Rahm* (1924) has shown that desiccated nematodes would survive an exposure to ÷ 190° C for more than 20 months and (1923) an exposure to ÷ 272° C for several hours. My own experiments have shown that desiccated individuals of *Plectus granulosus* are able to withstand + 66° C for at least four days.

Consequently a certain species of nematode may be expected to occur in nearly all types of locality at least in restricted numbers. A rough survey of the statements in the preceding chapter confirms this.

Thus it is necessary only to consider the species which have been obtained in such large numbers in the single localities that the numbers alone warrant the conclusion that the species are true inhabitants of the locality and not merely accidental visitors. In practice the number and the constancy are the only means available for a decision of the question. This fact in conjunction with the order of size of the animals necessitates that the points of view adopted should be identical with those applied to the distribution of protozoa and not to those applied to arthropods.

In order to reduce the errors of interpretation the general discussion can only comprise the more numerous and constantly occurring species. The lower limit of relative numerical importance chosen here is the same as that used in drawing up the tables of the previous chapter, namely that only those species are considered which independently constitute 1 % or more of the total number of individuals in each locality. It is admitted, that this percentage is arbitrary and no special property is ascribed to it except its being practical.

On this basis it is possible to carry out a certain grouping of the nematodes. It is a fact pointed out by all authors who have been occupied in the study of different groups of freeliving nematodes that two distinct cathegories may be

distinguished namely the marine species and the species of freshwater and soil with practically no species in common; often the limit is so sharp that this applies to genera or even families.

In the material presented here the following typical marine species were found on the outer part of the beach, where the sand is wetted with sea water: *Dorylaimopsis punctatus, Theristus setosus* and *Paracyatholaimus proximus. Dorylaimus balticus* and *Mononchus rotundicaudatus* have until now been found as a few specimens and these restricted to beaches; probably they are related to *Dorylaimus carteri* and *Mononchus brachyurus* respectively. *Choanolaimus psammophilus* is an interesting species which, I believe, bears the same relation to the marine species as do the soil nematodes to the exclusively freshwater species. It is never found on the sea bottom but only in the sand of dunes and shore beaches. As far as I know this is the only species which can be considered a soil nematode of marine origin. The opposite point of view that *Choanolaimus* might be an original soil nematode adapted to this special biotope is rather improbable as all the other *Choanolaiminae* and most *Chromadoridae* are typically marine species.

In the following discussion these marine species are left out of consideration. All the remaining species occur in the soil being more or less abundant.

Among these a group is constituted by *Plectus rhizophilus*. In a previous paper (1948 b) it was shown that this species represents 58 % of the nematodes found in moss cushions while it is insignificant in the soil.

Rhabditis monhystera, Rh. sp., Panagrolaimus rigidus and *Macrolaimus crucis* cannot be considered typical soil nematodes. They occur very irregularly, in most samples they are not present at all, however, when they occur, they are often found in very large numbers. As far as can be made out they are especially associated with putrefying substances such as rotting plant remains, dead earthworms, insects etc. In several of the tables it is seen that even if they constitute a fairly large proportion of the total number, their constancy percentage is generally low.

In this way 11 species are excluded, the remaining 59 species alone are considered as belonging to the typical soil fauna.

In an ecological study of a certain animal group it is very important to get an impression of the factors which determine the type of distribution of the species. However, a clear picture is rather difficult to obtain because a certain factor may be operative either isolated or in conjuntion with others, which in many cases are not at all evident.

On account of the very great variations a large amount of material is necessary in order to show up the single factors. In my case only some few important

factors could be isolated, while the remaining will probably turn out to be more reliably studied by means of experiment.

As a basis for discussion I have tried to give some typical values of number and weight per sq. m. in 4 representative soil types:

1. Sand. The values were obtained by a calculation of the average from the Plain I + II (table 2), the grass fields of table 7 (st. I—V), and the grass fields of table 8. In all cases the soil consists of sand with a small dredgeable fraction.

The vegetation consists of grasses with a moderate to high degree of cover. All extreme localities (the beach, *Corynephorus* slopes, the sandy meadow and other localities examined) were excluded in order to obtain a picture as typical as possible.

2. Clay soil. The limit between this type and the preceding one is a matter of convention, thus an extreme clay must be chosen. In fact the heaviest one which I have examined served as a representative (table 12, 3 last columns). The vegetation corresponds fairly well to that of the sandy grass fields.

3. Raw humus. The localities with a raw humus layer less than 5 cm thick had to be avoided. The *Calluna* and *Vaccinium* raw humus (table 13) and the spruce and fern raw humus (table 14) were used as a basis in calculating an average population.

4. Peat. The main difference between this and the preceding type is found in the water status. The localities chosen here are those from table 15, which are permanently water logged.

The values thus obtained have been set out in table 17*. The numbers can be compared directly, as they represent number in thousands and weight in mg and g per sq. m. from each of the four types. When this way of presenting the material is chosen the main features of distribution are clear cut:

1. One large group of nematodes (No. 1—19) occur abundantly in almost all types of soil, except some species (No. 9—19) which are not recorded from the peat localities and 7 species (No. 11—17) not found in the raw humus. In reality they occur both in raw humus and in peat but only in small numbers, the blanks in the table thus not being of fundamental importance.*) In other words those 19 species may be expected to occur in a random sample irrespective of the type of soil, a fact which is confirmed by general experience.

2. The species *Tripyla setifera, Acrobeles ciliatus* and *Tylencholaimus mirabilis* (especially the two latter species) are confined or nearly so to sandy soil provided this is not permanently water logged.

3. The species *Acrobeles vexilliger, Wilsonema otophorum* and *Bunonema*

*) This is easily verified by the tables given by *Micoletzky* (1921), *De Coninck* (1930) and *Overgaard* (1948 b, the soil samples p. 93—95).

reticulatum (as well as *B. richtersi)* are typical of raw humus i. e. in this type of soil they occur regularly and often in great numbers. In contrast with the preceding group they are not exclusively confined to this soil type as *A. vexilliger* and *W. otophorum* often occur in sand, especially in dry localities, while *B. reticulatum* and other *Bunonema spp.* also occur regularly in moss cushions on raw humus and—in small numbers—in peat.

4. From peat a series of species (no. 26—39) has been recorded. None of them were found in any of the other soil types included in the table. Nevertheless they do not represent a special "peat community". A comparison with tables 10, 11, 15, and 16 shows that the species in question occur in sand and mull meadows as well as in peat and bog soil provided the soil is permanently moist. In the bottom deposits (mud as well as sand) of Rind Aa adjoining the locality of table 10 *Monhystera filiformis, Dorylaimus limnophilus, D. stagnalis, Mononchus macrostoma* and *Tripyla papillata* were abundant together with some other typical freshwater species not found in the soil samples.

It is thus evident, that the species mentioned here may be found in freshwater as well as in permanently moist soil of widely different type, from pure sand to soil without mineral components (peat, bog soil). This point of view is supported by records from the literature. *De Man* (1884) lists *Dorylaimus longicaudatus* and *D. brigdammensis* among the "meadow"" species. Among *Micoletzky*'s (1921) exclusively freshwater species we find *Chromadora ratzeburgensis, Ironus ignavus, Teratocephalus palustris* and *Trilobus gracilis.* Among his species which are 10—25 times as common in freshwater as in soil *Dorylaimus stagnalis, Rhabdolaimus terrestris* and *Ethmolaimus pratensis* are found. *Mononchus macrostoma* belongs to the preferably freshwater species while *Monhystera filiformis, Tripyla papillata* and *Monhystera vulgaris* are amphibious species somewhat more abundant in freshwater. *De Coninck* (1930) has: Typical freshwater species: *Achromadora ruricola, Dorylaimus stagnalis, Ethmolaimus pratensis, Mononchus macrostoma* etc. Amphibious species: *Aphelenchoides parietinus, Panagrolaimus rigidus, Dorylaimus brigdammensis, D. carteri, D. obtusicaudatus, D. tritici, Monhystera filiformis, Plectus cirratus, Prismatolaimus dolichurus, Tripyla papillata, Rotylenchus robustus* etc.

It is evident that the ecological range of many nematodes is extremely large. Thus e. g. *Dorylaimus obtusicaudatus* occurs in freshwater in large numbers as well as in all localities examined by me — in the extremely dry, bare *Corynephorus* slopes it constitutes 40 % of the individuals corresponding to 70 000 individuals per sq. m. (= 700 mg). In other species the range is smaller. In the group under consideration here it comprises only water and permanently moist soil.

5. In clay soils I have not been able to find a special fauna, all the species occurring here are identical with those of sandy soil. This fact is also evident from

table 17. In constantly moist clay e. g. at the border of marl pits the fauna is very poor while it qualitatively corresponds closely to that of moist sand, peat and bog soil (*Mononchus macrostoma, Dorylaimus limnophilus, Tripyla papillata, Chromadora ratzeburgensis* and *Chr. leuckarti* were the most common species in such a locality near Studsgaard).

It appears from table 17 that the ecological valency of several species is wide, while a few (framed in the table) are confined to certain types of environment. However, this conclusion was reached on the basis of calculated average populations. To demonstrate the validity of the conclusion in the case of actual localities table 18 was compiled. In the table all the localities mentioned in the preceding chapter are listed vertically and all the dominants (except those which belong to the groups framed in table 17) horizontally. The crosses (x) indicate the distribution of the dominants in the localities. It is seen that only 21 eurytopic species occur as dominants among ca. 100 possible in 34 localities. Here it must be remenbered that my concept of a "dominant" means that the 2—3 dominants of a locality together constitute half the population, the species thus being really important.

If, instead of my concept of a "dominant" that of *Krogerus* (see p. 21) is applied to these important species my dominants become common to still more localities, namely all those marked "x" and "o", constituting at least 5 % of the fauna of the various localities. If the localities are also considered where the species are influent (i. e. constituting 2—5 %) the qualitative composition of the fauna becomes still more homogeneous. These localities are marked " □ ".

In addition to this wide distribution it must be stressed that the constancy percentages are generally high, however, they cannot be compared directly as the samples are not of equal size.

On account of the general agreement between the fauna of sand and clay this latter soil type will be left out of consideration. In this way the following discussion can be restricted to sand, raw humus and peat.

The fauna of these three soil types was in all cases found to consist of an eurytopic component and a group of species practically confined to this soil type.

In table 19 the importance of eurytopic and stenotopic species is shown in all three types; the percentages are given on a numerical as well as on a weight basis.

The main purpose of this paper being to give an analysis of the nematode fauna especially from a metabolic point of view, the emphasis must be placed upon the weight statements. Consequently, on the basis of table 17 we reach the conclusion that in typical sandy soil and raw humus with a fairly close plant cover the eurytopic species constitute about 95 % of the total weight. In peat and all other per-

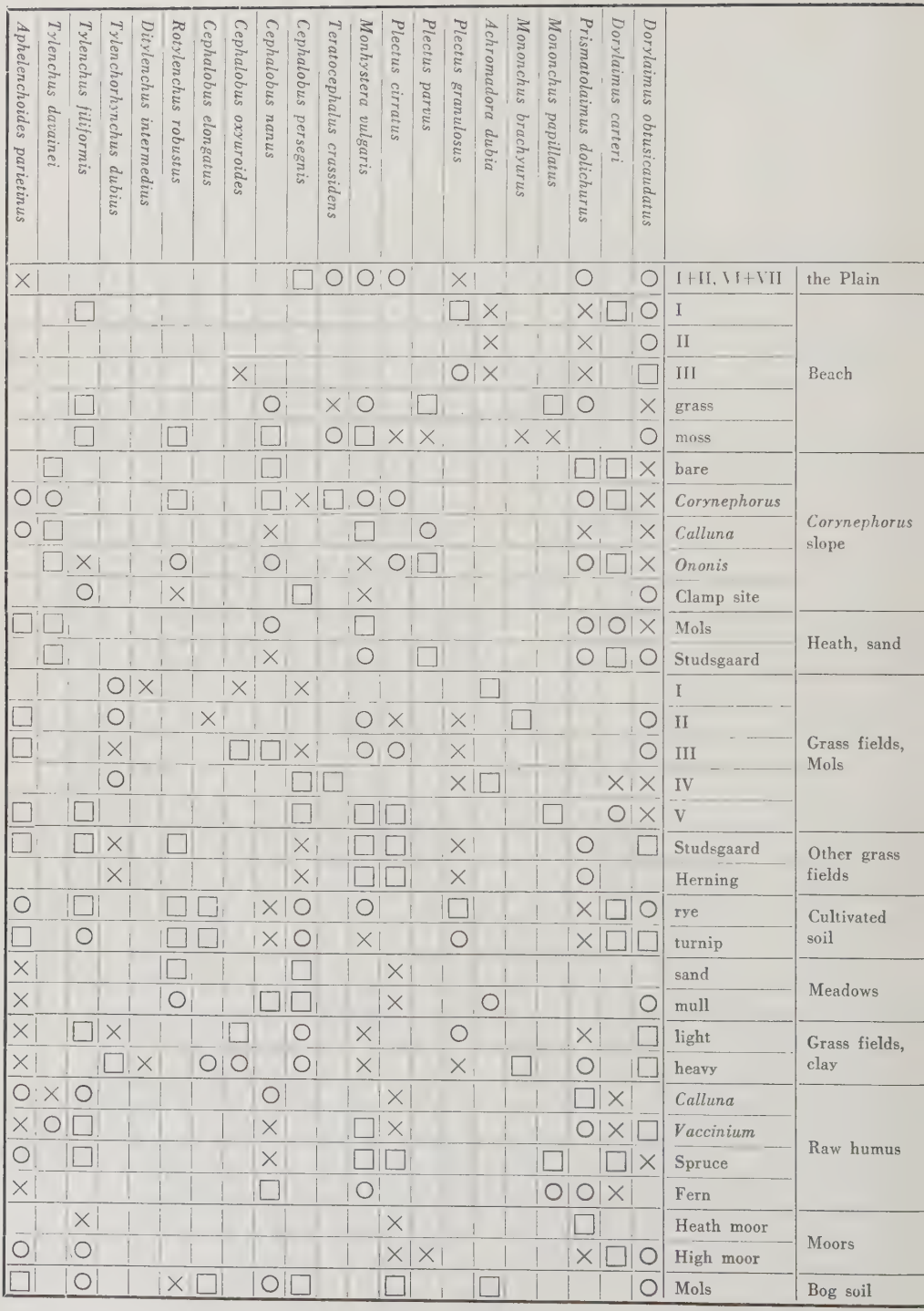
Aphelenchoides parietinus
Tylenchus davainei
Tylenchus filiformis
Tylenchorhynchus dubius
Ditylenchus intermedius
Roylenchus robustus
Cephalobus elongatus
Cephalobus oxyuroides
Cephalobus nanus
Cephalobus persegnis
Teratocephalus crassidens
Monhystera vulgaris
Plectus cirratus
Plectus parvus
Plectus granulosus
Achromadora dubia
Mononchus brachyurus
Mononchus papillatus
Prismatolaimus dolichurus
Dorylaimus carteri
Dorylaimus obtusicaudatus
I+II, VI+VII
the Plain
I
II
III
Beach
grass
moss
bare
Corynephorus
Calluna
Ononis
Corynephorus slope
Clamp site
Mols
Heath, sand
Studsgaard
I
II
III
Grass fields, Mols
IV
V
Studsgaard
Herning
Other grass fields
rye
turnip
Cultivated soil
sand
mull
Meadows
light
heavy
Grass fields, clay
Calluna
Vaccinium
Spruce
Fern
Raw humus
Heath moor
High moor
Moors
Mols
Bog soil

Table 19.

	percentage importance in		
	sand	raw humus	peat
eurytopic species on numerical basis	90	83	48
eurytopic species on weight basis	**95**	**95**	**23**
stenotopic species on numerical basis	3	14	46
stenotopic species on weight basis	**3**	**3**	**76**
less important species (no. 40—54)			
on numerical basis	7	3	7
on weight basis	**2**	**2**	**1**

manently moist localities, irrespective of the soil type, these species are much less important only constituting about 25 % of the weight while the specific group constitutes about 75 %. In all localities the group below the horizontal line in table 17 is really unimportant as it only constitutes 2, 2 and 1 % of the weight in sand, raw humus and peat respectively.

When we leave table 17 to regard the composition of the fauna in some actual localities several exceptions are found especially in the extreme localities.

Sand. In extremely dry localities e. g. the bare *Corynephorus* slopes the total number per sq. m. decreases to about 175 000 (= 1 g) and the number of species is low (10). It is typical of these extreme localities that the proportion of the species restricted to sand increases. On a numerical basis they constitute 16—56 % and on a weight basis 6—16 % in the different sections of the *Corynephorus* slopes. In the dry *Calluna* heath at Strandkjær and Studsgaard the numerical percentage is 45 and 28 respectively while the weight percentage is 19 and 18 resp.

Towards the optimum localities with a closed plant cover the proportion of these species decreases on account of an increase in the total population of the locality resulting in a greater number of species as well as of individuals. In several cases the absolute number of the species restricted to sand also decreases in the richer localities (where the humus content is generally higher). At Plain I + II and VI + VII we have a total population of 10 million per sq. m. while *Acrobeles ciliatus* and *Tylencholaimus mirabilis* on an average constitute 3 % of the individuals and 1.5 % of the weight. In the luxuriant grass fields at Studsgaard and Herning, where the total fauna amounts to about 20 million the species in question are totally absent.

In the permanently water logged localities the fauna is poor (1—2 million = 1—2 g) and the composition of the fauna corresponds closely to that of peat.

Raw humus. This soil type shows only small variations as is seen from table 13 and 14 both with regard to the species composition and the total population which almost invariably lies between 1 and 3 million per sq. m. corresponding to a weight of 1—4 g. The fauna of *Calluna* raw humus (table 13) does not differ essentially from that of a *Calluna* heath on sand (table 6). Most species in these two types of locality belong to the eurytopic group.

The group of nematodes which is mainly restricted to raw humus shows only a small variation in percentage importance (in the 4 localities ranging from (numerically) 5—21 % and on a weight basis the importance is practically negligible because the three species in question are very small — *Acrobeles vexilliger* weighs 0.5 γ *Wilsonema otophorum* 0.1 γ and the *Bunonema spp.* ca. 0.02 γ. *Bunonema* occurs somewhat irregularly and is far from universally present. *Wilsonema otophorum* may also occur in sand, especially in dry localities (e. g. at st. IV of table 7 where it amounts to 83 000 per sq. m. = 2 % of the total fauna and corresponding to 8 mg (= ca. 0.1 % of the total weight).

Permanently moist localities. While the species composition of the faunas of sand and raw humus are much alike apart from the two groups of species restricted to each of them, the fauna of peat and all other permanently moist localities is fundamentally different. The total fauna is small, practically never exceeding 2 million per sq. m. corresponding to 1—2 g. In principle the species composition shows two components, an eurytopic soil and a stenotopic freshwater group among which the latter one is generally the most important with regard to weight, 48—60 %, while the soil component dominates numerically, 51—66 %.

Cultivated soil. The current opinion that a richer fauna is found in cultivated soil as contrasted with virgin soils could not be confirmed. According to my experience the cultivated soils must be placed in the same cathegory as virgin soils with a corresponding density of the vegetation. Immediately after stable manure has been applied a large number of nematodes may be found, however, in the course of very short time this surplus again disappears and the fauna returns to its original size. With regard to species this "dung fauna" (see *Paesler* (1946)) also differs from that of natural soil as a great number of *Rhabditis spp., Cephalobus elongatus, Panagrolaimus rigidus, Diplogaster spp.* etc. occur. The rather large number of *Rhabditis monhystera* in the cultivated soil of table 9 may originate from this source.

In cultivated and virgin grass fields of similar degree of cover and water conditions the number of individuals is similar (upwards of 20 million in the case of dense vegetation) (table 8). When the vegetation is open the number is generally lower (2—10 million) and leaving the grass fields a similar number is found in fields grown with other plants. In the rye field (table 9) the fauna seems to

be twice as dense (2.5 million) as in the turnip field (1 million) on the same soil type.

A difference between virgin and cultivated soil occurs in the vertical distribution of the fauna to be discussed in the following chapter.

Even if the degree of cover of the vegetation and the density of the nematode population seem to be directly correlated it cannot be decided whether they are causally related or each of them result from a common third factor or several other factors. The problem is further discussed in chapter 10.

6. THE VERTICAL DISTRIBUTION OF THE FAUNA

In the literature the density of the nematode fauna has not been analysed in a complete soil column reaching from the surface to the water table. For practical purposes such an analysis is of restricted value because the nematode fauna which is of importance is that confined to the upper layers, where the root net of plants is found. Nevertheless an analysis of the complete vertical distribution can throw a certain light on theoretical questions.

At st. I on the beach (see fig. 1) such an analysis was undertaken by extracting the fauna from a sample series consisting of 80 samples each of 1 sq. cm area and 5 cm height. 5 samples represented each of the depths 0—5, 5—10, 10—15 and so on until 75—80 cm where the water table was located.

The total fauna per sq. m. amounts to 510 000 in the layers 0—80 cm, a very small number in comparison with most other localities. If the percentage distribution in the different depths is analysed the diagram fig. 4 *a* is obtained. Two maxima are present: 1. 5—20 cm below the surface with 24 % of the total fauna — here also a root maximum occurs — and 2. 10—35 cm above the water table with 66 % of the total fauna. Between these two maxima a distinct minimum is found comprising only 10 % of the fauna. No qualitative differences were found between the different depths.

A determination of the water content (based on dry weight) shows (fig. 4 *b*) that 18 % water is present at the water table, 10 cm above the percentage has decreased to 9 and from 20—60 cm above the water table 5 % water is present. From 60—70 cm the water content decreases from 5 to 1 % and in the layer 70—80 cm above the ground water (= a surface layer 10 cm deep) the water content is 0.05 %. The greatest water content is found in the water-bearing layers at about 80 cm depth. By capillarity the water may rise ca. 25 cm in sand of this grain size according to *Atterberg* (1903). This zone with capillary water ranges consequently from 5—30 cm above the water table i. e. precisely corresponding to the lower maximum. The water present in the layers

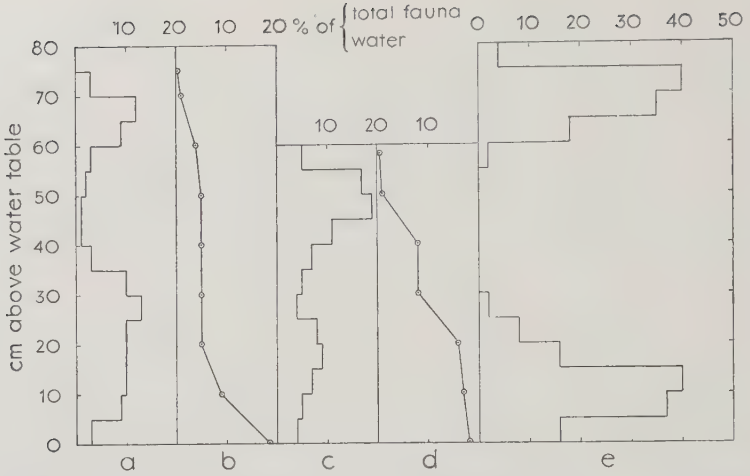

Fig. 4. Vertical distribution of nematodes from water table to surface in % of the population of the total soil column on the beach at *a* station I, *c*. st. III. Water percentage (based on dry weight) at *b*. st. I and *d*. st. III. *e*. Vertical distribution of proturans (above) and harpacticids (below) in % of the total populations at st. I.

elevated more than 25 cm above the water table, i. e. in the depths from 0—45 cm, must originate from the surface.

In fig. 4 *c* a parallel diagram from st. III of the same line (see fig. 1) is shown. The main difference is that the distance between the surface and the water table is 20 cm less. Here also we find two maxima: 5—15 cm below the surface and — less distinctly — 5—25 cm above the water table. The "compression" of the profile has caused the intermediate minimum to become less distinct. The water conditions at this station remind one very much of those of the preceding one: 0—20 cm above the water table: 18—16 % water, 20—30 cm: 16—8 %, 30—40 cm: 8 %, 40—50 cm: 8—1 %, 50—60 cm: 1—0.4 % (fig. 4 *d*). The higher percentage in the upper 10 cm is due to the fact that splashes from the waves reach this station.

Fig. 4 *e* represents the percentage distribution in the vertical direction of proturans (above) and harpacticids (below). A discussion of this diagram is given in the following chapter (p. 65).

In the pure sand of the beach the soil conditions are very simple on account of the homogeneous single grain structure and the absence of organic matter and clay. The conditions prevailing here cannot be directly applied to more complicated soil types, however, such a locality is almost ideal for the elucidation of certain major factors, which are operative without the several combinations occurring in most other soils.

In most localities the eventual lower maximum is not accessible in practice,

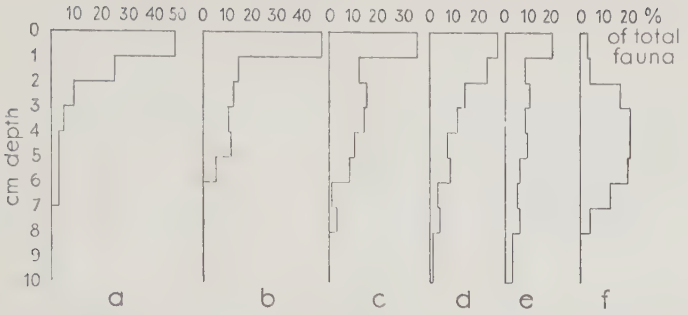

Fig. 5. The vertical distribution of nematodes in % of the total fauna in *a.* the Plain I + II, *b.* the *Corynephorus* slopes under *Ononis*, *c. the Corynephorus* slopes under *Calluna*, *d.* the bog soil of the Plain, *e.* the rye field at Studsgaard and *f.* the bare *Corynephorus* slopes.

on the whole I doubt very much its universal presence. At least it is absent in the Plain, where the fact could be verified.

When the vertical distribution within the upper maximum is examined it is found that its position in relation to the soil surface is different in different biotopes.

Generally the largest percentage of the total population is found within the layer 0—1 cm decreasing with depth to a total absence of nematodes somewhere about 20 cm depth.

Fig. 5 *a—f* shows the actual percentage distribution of the nematodes in a soil column from different localities. At Plain I + II (table 2) 49 % of the fauna is concentrated in the layer 0—1 cm and about 90 % in the upper 5 cm. In the bog soil of the Plain (table 16) 28 % is found in the upper 1 cm and about 85 % in the upper 5 cm. On the *Corynephorus* slopes (table 5) the following results were obtained: Under *Ononis:* 47 % in 0—1 cm, ca. 95 % in 0—5 cm, under *Calluna* 35 % in 0—1 cm, 85 % in 0—5 cm, in the *Corynephorus* zone: 3 % in 0—1, 65 % in 0—5 cm. In the cultivated soil of the rye field (table 9) 19 % were concentrated in the layer 0—1 cm and 77 % in 0—10 cm.

In principle three main types of vertical distribution may be discerned with all intermediate conditions, however: 1. The main part of the fauna is concentrated near the surface and decreases with depth until the nematodes disappear completely at about 20 cm depth. This is the most usual type occurring in almost all virgin soils which are covered by vegetation irrespective of the locality being permanently moist (bog soil fig 5 *d*, table 16; meadows, tables 10 and 11; peat, table 15) or not (the Plain I + II, fig. 5 *a*, table 2; the Plain VI + VII, table 2; the *Corynephorus* slopes under *Ononis* and *Calluna*, fig. 5 *c*, *d*, table 5; the *Calluna* heath, table 6; the grass fields, tables 7, 8 and 12; the raw humus, tables 13, 14. When a

sampling depth of 5 cm is employed about 90 % of the total fauna is obtained. 2. The fauna shows a maximum ca. 5 cm below the surface and decreases upwards as well as downwards. This distributional type is usual in places where the vegetation is open or absent and the evaporation is great (the beach fig. 4 *a, c,* table 3) and the bare or nearly bare areas of the *Corynephorus* slopes (fig. 5 *f,* table 5). It is interesting to note that the upper areas of the beach (table 4) show this type of distribution in the case of an open grass cover, below the moss cushions, however, the fauna decreases evenly from the surface downwards. When using a sampling depth of 10 cm nearly 100 % of the fauna is obtained. 3. The fauna is more evently distributed within the upper 20 cm only showing a slight decrease with depth. This case is met with in cultivated soil (fig. 5 *e,* table 9). When using a sampling depth of 10 cm ca. 80 % of the total fauna is obtained.

From this survey it becomes evident that when different localities are compared, the vertical distribution must be examined in each case and the sampling depth chosen according to this analysis. The sampling depth used for this paper was 0—5 cm in most cases (the vertical distribution being of the first type); in some few localities where the vertical distribution conforms to the second or third type a sampling depth of 0—10 cm was employed. In doing so 80—100 % of the total fauna of the sample area is obtained. This fact must be taken into consideration when—in chapter 10—the importance of the nematodes is discussed on the basis of the total number of animals per sq. m.

Besides this practical purpose also a theoretical question arises, namely the reason for the differences in vertical distribution.

The vertical distribution corresponds fairly well to that of most other components of the microfauna. Concerning arthropods *Morris* (1922) and *Frenzel* (1936) found 70 % of the fauna to be concentrated in the upper 5 cm while *Weis-Fogh* (1948) found 70 % of the mites and collembola in the layer 0—1 cm on the Plain. In freeliving nematodes a similar conclusion was reached by *Franz* (1942).

As will be explained in the following chapter the presence of water must play an important role for nemadodes, but it cannot be the sole factor. Most organisms of the soil generally occur in greatest number near the surface, at least there is no doubt that this is a fundamental type of distribution and it can easily be imagined that conditions are really optimum here. It would be meaningless to demonstrate the effects of the single factors, because factors are rarely single in nature.

The second type of distribution is in the same way due to a complex of factors. It might be tempting to explain the absence of nematodes from the upper 5 cm of the beach by the fact that the sand is often completely dry and consequently unsuitable for nematode activity. However, this is probably not the sole factor.

Moore (1931) found exactly the same type of distribution in marine nematodes of the Clyde sea area (depths 24, 73 and 166 m). On the other hand *Moore*'s explanation of this type of distribution on the sea bottom by ascribing to nematodes the power of anaerobic existence does not solve the problem on the beach.

The third type of distribution which occurs in cultivated soil may partly be explained by the effect of ploughing and other soil treatments. During this process not only is the fauna mixed up within the ploughing depth, but the same applies to most environmental factors.

It may be summarized that the distribution of nematodes within the upper maximum is in conformity with that of several other soil organisms where the question has been investigated, e. g. bacteria, actinomycetes and fungi (see e. g. *Waksman* and *Starkey* (1931)) and algae *(Boye Petersen* (1935)). The location of the maximum will correspond to the horizon with optimum conditions for the activity of microorganisms in general. This optimum is probably an integration of several factors such as nutrition, moisture relations, temperature, aeration etc.

With regard to the vertical distribution of nematodes in cultivated soil my findings are in agreement with those of *Franz* (1942).

7. THE MOISTURE RELATIONS OF THE SOIL MICROFAUNA

In the older literature the soil structure was represented in a very schematical way. Today the schemes may persist, however, not as the final analysis but as a frame within which the detailled analysis is carried out, an analysis which has become possible to a large extent on account of recent progress in physical chemistry, colloid chemistry, x-ray analysis and the energetical concepts of soil moisture. The theoretical questions cannot be touched upon here, but several facts are apt to modify the concepts of soil biology. These must be considered, while for further details the reader is refered to the special literature among which may be mentioned *Kubiena* (1938) and *Baver* (1940) where further references are given.

Firstly we will have to define the word "microfauna". In systematics the species and different cathegories of species of higher or lower rank are defined on a taxonomical basis. In ecology the units and groups of units must be defined in relation to the environment. This is difficult and it necessitates a labile framing. It may be expected that the same species behave differently in different environments.

In the case of the soil fauna two groups are often distinguished in an ecological respect, namely the microfauna and the macrofauna. The limit between these two groups is a matter of convention, in principle the only difference is that the "microfauna" consists of animals which are small in comparison with those of the

"macrofauna". To make confusion still worse a third group has been distinguished, namely a "mesofauna" which is to comprise some animals characterized by being larger than the members of the "microfauna" and smaller than those of the "macrofauna". Originally all the limits were fixed according to arbitrarily chosen measures. In practice, however, the classification has become illogical as e. g. the term "microfauna" is thought to comprise some definite taxonomical groups, the species of which will g e n e r a l l y not exceed a certain size e. g. 1 mm length.

Everywhere in this paper the microfauna is defined so as to comprise all the animals which are small in comparison with the structural elements of the soil where they live, i. e. the members of the microfauna will utilize the capillaries and cavities already present, while they are unable to produce holes and burrows of their own. It follows that the microfauna has no mechanical influence upon the nature of its evironment, in contrast with the macrofauna. Another consequence is that one single species may belong to the microfauna in one locality and to the macrofauna in another one, and this is rightly so. Direct observation has revealed that the freeliving soil nematodes are real microfauna elements in the soils examined by me, while on the other hand a marine species *Pontonema vulgare* is a typical macrofauna animal in mud deposits and a microfauna animal in sand*).

Next the question arises: what is the environment of the soil microfauna? The composition of a silt loam may be represented as 50 % solids (among which mineral substances constitute 45 and organic matter 5 %) and 50 % pore space (of which 30 % may be water and 20 % air) all the percentages being based on volume *(Lyon* and *Buckman* (1947)).

Some organisms utilize the mineral and organic substances as food and (or) a source of energy. In other organisms they may serve to stabilize the merely physical and chemical environment (osmosis etc.) or they may not be significant.

By an appropriate medium I understand an environment where all the vegetative and animal functions of the different members of the soil microfauna can be maintained. This medium is different when the entire microfauna is considered. The arthropods constitute an a e r o p h i l o u s group which depends upon the air phase of the soil, while protozoa, turbellaria, nematodes, rotifers and tardigrades constitute a h y d r o p h i l o u s group dependant upon the water phase and being unable to maintain normal activity in an evironment without free water.

From this it is seen that the problems pertaining to soil moisture are important and derserve special attention and ecological interpretation when analysing the environmental requirements of the freeliving soil nematodes**).

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*) Similar points of view with regard to classification of the organisms of the soil are held by *Stöckli* (1946 a) and, in the case of arthropods, by *Weis-Fogh* (1948).

**) In botanical ecology the questions have been studied intensively and have even been included in common agricultural pratice. For a survey and further references see e. g. *Braun-Blanquet* (1932), *Daubenmire* (1947) and *Lyon* and *Buckman* (1947).

In ecological papers the authors have often carried out careful determinations of the water content (based on fresh or dry weight) without giving a detailed analysis of the nature of the soil. Such statements do no explain the moisture conditions. This applies in the case of single measurements e. g. in connection with the sampling and also where regular measurements are at hand, and the reason is that the water which is active biologically constitutes a fraction only of the total amount of water found by such analyses.

An airdried soil absorbs water vapour from an atmosphere containing water vapour. This absorption is due to a power of attraction exerted by certain molecules of the surfaces of the particles. A soil balanced against an atmosphere of 100 % r. h. will absorb more water than one balancing with an atmosphere of say 50 % r. h.

A soil sample as a thin layer heated to 105° C for 12—16 hours is considered water free *(Piper* (1944)) (in reality it contains an exceedingly small amount of water), say the sample weighs a g. On transfer to an atmosphere of 100 % r. h. it absorbs water. When an equilibrium is reached the weight has increased to b g.

The fraction $\frac{b \div a}{a}$ gives the maximum hygroscopicity (= unfree water *(Bouyoucos* (1921), hygroscopic water *(Briggs* (1897) of the soil in question and $\frac{100\ (b \div a)}{a}$ the corresponding water content in % of dry weight. At maximum hygroscopicity water is withheld in the soil with such a great energy that very few organisms are able to utilize it as the osmotic pressure would have to exceed the tensional force (see e. g. *Stiles* (1936)).

The hygroscopic water constitutes a film which is thought to be made up of 15—20 layers of water molecules and of a thickness of 4—5 m μ. On account of the enormous tensions fixing these layers (at the interfaces approaching 10 000 atmospheres) the molecules are closely packed and partially non-liquid. With increasing water content the tension approaches that of surface tension. In soils with small organic content the hygroscopic water generally represents 1—2 % but may rise to 12—15 % in soils more rich in organic matter and clay (particle size $< 1\ \mu$). In peat and raw humus it may even increase to about 70 % of the dry weight *(Lyon* and *Buckman* (1947)).

When free water is present bacteria, protozoa, nematodes, turbellarians, tardigrades and rotifers may eventually be active because they are in contact with water films. By free water I understand the water present in a soil in excess of the hygroscopic water (= capillary + gravitational water *(Briggs)* = free water + gravitational water *(Bouyoucos)).*

From the above it appears that, in the case of the hydrophilous animals

the mere measurement of the water percentage is of restricted value. Probably the most convincing illustration is obtained when identical amounts of water are applied to identical volumes of three different types of soil. The calculations have been made on three actual soils described by *Schübler:*

I. Sand. Volume weight 1.5, specific gravity 2.65, pore volume 43 %. Maximum hygroscopicity 2 %.

Thus 1 cc of sand contains 430 μl pores. After addition of 250 μl water (= 25 vol. %) 220 μl free water is present.

II. Silt loam. Vol. weight 1.5, specific gravity 2.65, pore volume 43 %, maximum hygroscopicity 10 %.

Thus 1 cc of silt loam contains 430 μl pores. After addition of 250 μl water (= 25 vol. %) 100 μl free water is present.

III. Raw humus. Vol. weight 0.5, specific gravity 1.4, pore vol. 36 %. Max. hygroscopicity 60 %.

Thus 1 cc of raw humus contains 360 μl pores. After addition of 250 μl water (= 25 vol. %) free water is absent, the maximum hygroscopicity not even being reached.

In natural localities conditions are more complicated, not all free water (= total water ÷ hygroscopic water) being accessible, as part of it is bound up in living organisms, especially roots. *Weis-Fogh* (1948) found that in Plain I the root water constituted 1/2 of the total water in the layer 0—1 cm 1/3 in the layer 1—2 cm decreasing to 1/8 in the layer 4—5 cm. In Plain VII it constituted 1/2 in the layer 0—2 while it decreased to 1/10 in the layer 4—5 cm. Thus the accessible water may in certain cases constitute a small fraction only of the total water. Furthermore the accessibility is dependant upon the nature of the organisms in question, thus it cannot be discussed with regard to all groups of soil organisms simultaneously. Here the discussion is confined to the soil microfauna. On p. 58 it was mentioned that an aerophilous and a hydrophilous group may be distinguished, the former mainly consisting of arthropods and the latter among others of nematodes. Of course, either of the groups require water to maintain normal activity, but it must be stressed, that the hydrophilous animals require water as a medium, which is not the case in the other group. Thus the moisture requirements are widely different in these two components. Accordingly different types of distribution of the two groups may be expected and they are, in fact, apparent horizontally as well as vertically.

On p. 59 it was mentioned that raw humus has a very high hygroscopicity, in addition it swells very much during moistening. In not permanently moist raw humus this involves a reduction of the accessible water, which is especially harmful to the animals, that utilize the water as a medium. The aerophilous

microarthropods are extremely numerous in this soil type (see e. g. *Forsslund* (1943) and *Weis-Fogh* (1948)) where their fundamental requirements are satisfied: food (to a large extent consisting of fungi and "humus"), water (mostly ingested together with the food) and an atmosphere with a certain amount of water vapour (in most cases the air is almost saturated with water (see *Thamdrup* (1939)). The number of nematodes in this type of soil is always small in comparison with mineral soil, probably because the water ingested with the food is not sufficient for these animals. In addition they require water as a medium. However, the amount of accessible water is small as one large fraction is hygroscopical and another large one bound up in living organisms (probably fungi are at least as important as roots here). In the very dense raw humus the small pore size (reduced by swelling) may perhaps be an important factor too. It may be mentioned that the smallest freeliving nematodes (*Bunonema spp.* and *Wilsonema otophorum)* are typical of raw humus together with *Acrobeles vexilliger* which is also rather small (0.5 γ) (see table 17).

In mineral soils relatively more accessible water is present and here nematodes are more important than microarthropods (this question is discussed p. 108).

Thus a decreasing amount of water will not affect the aerophilous microanimals seriously until a limit has been reached where the relative humidity of the soil air has decreased below a certain value which is different according to species (see e. g. *Agrell* (1941) and *Backlund* (1945)). In the hydrophilous group activity may be continued until the water films have disappeared. After this the nematodes and most others become inactive, entering an anabiotic state.

An increasing amount of water will not affect the aerophilous group seriously until so much water is present that the animals are in fear of drowning. As long as water films are present an increase of the water content will favour the activity of nematodes. However, when the soil becomes permanently water logged probably the n u t r i o n a l conditions are impoverished on account of the reduction of water-air interfaces with a consequent reduction of microbiological activity. At least this is the only way in which I am able to explain the fact that the nematode density of freshwater and sea bottom is always low in comparison with that of soil in spite of the fact that soil nematodes are, according to nature, aquatic animals. This fact is apparent on comparing soil and freshwater statements in the literature, and it was confirmed by personal investigation. As an example fig. 6 is given showing a transect of the outer part of the meadow bordering Rind Aa, a rivulet in western Jutland, together with two samples from the bottom deposits (the same locality is analysed p. 36). Ca. 50 m from the bank the soil is not permanently moist and the nematode density amounts to 14 million per sq. m. Two meters from the bank the soil is much more moist, while the fauna has decreased to ca. 2 million ond on approaching the bank further the soil be-

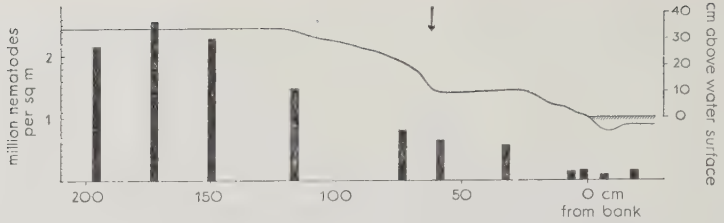

Fig. 6. Transect of the outer part of the meadow bordering Rind Aa showing the relation of nematodes and water content of the soil. Approaching the bank (to the right) the soil becomes still more moist, from the point indicated by an arrow it is permanently water logged. In the bottom deposits of the rivulet and in the meadow next to it the nematode fauna is considerably poorer than in the more distant parts of the meadow (see text).

comes water logged ca. 1 m from the rivulet where the fauna has decreased to less than 1 million. At the water edge only 100—200 000 nematodes were present per sq. m., and this number was found in the bottom of the rivulet too. Thus the fauna is of the same density as that of the extremely dry *Corynephorus* slopes, while it may be 100 times as dense in typical soils.

Thus in a moisture zonation ranging from extremely dry soil to freshwater we may distinguish in the case of arthropods a d r y s o i l f a u n a (e. g. in Plain I according to *Weis-Fogh*) and a m o i s t s o i l fauna (e. g. typically developed in Plain VII). In the case of nematodes we must distinguish a s o i l f a u n a (found throughout Plain I—VII) and a f r e s h w a t e r f a u n a, which does not appear until the soil has become permanently moist (e. g. in the bog soil of the Plain and which is characteristic quantitatively as well as qualitatively (see p. 52). The limit between these faunal elements is not identical. In nematodes it is located in more moist localities than in arthropods. This must be due to the different water requirements of the two groups which is confirmed by the fact that other hydrophilous groups show the same type of distribution as do the nematodes. Thus in Plain I—VII we find the usual soil inhabitants among the protozoa (many flagellates, several rhizopods and very few ciliates), among the rotifers only a few *Bdelloidea* and no turbellarians. In the bog soil these groups are much more diversified. Among the protozoa ciliates are important *(Colpoda, Colpidium, Enchelys, Amphileptus, Lionotus, Bryophyllum, Dileptus, Spirostomum, Stylonychia* etc.). Apart from the first two genera none of them occur in Plain I—VII. Rotifers are abundant too, apart from several *Bdelloidea* also *Colurella, Euchlanis* and *Monostyla* occur. The density of small turbellarians may be upwards of 100 000 per sq. m.

In most localities conditions become somewhat more complicated on account of the size of the microorganisms in relation to the size of the pores.

Weis-Fogh (1. c.) found a very close agreement between the size of the pores

in Plain I—VII and the size of the aerophilous microanimals which inhabit them, and *Stöckli* (1946) gives a general discussion of the problem.

If the pore size distribution is analysed it turns out that a varying fraction of the total pore space is made up by pores which are smaller than certain members of the soil microfauna. These pores cannot be used as a haunt for these animals, nor can the water in these pores be utilized as a medium. However, no general statements can be given as to the pore size which is required by the different soil microorganisms, it depends entirely upon the size of the organisms in question. The reduction of the traversable pore space (and water) due to this factor may be important. This is illustrated by *Donat's* (1937) measurements. In four different soils he found that the following percentages of the total pore space consisted of pores with an equivalent diameter of 20 μ or less:

Quartz sand, 0.5—1.0 mm	4 %
Clayey loam	96 %
"Scluff" sand	20 %
Field soil (Ackerkrüme)	63.5 %

While the pore size seems to be an important distributive factor in microarthropods it seems to be less important in nematodes probably because they are generally small — the diameter in most cases (except *Dorylaimus Mononchus* and a few others) being 20—50 μ. Perhaps the small size of the raw humus species may be interpreted in this way (see p. 61).

It is a general rule that the smaller the animals, the better are they fitted for living in the soil (if they are not able to burrow and consequently belonging to the macrofauna). In the aerophilous organisms it follows that a much larger total pore volume is traversable. The same applies to the hydrophilous organisms (also the microflora) but in addition these organisms obtain a much more constant medium when they are small, because the water confined to the smallest pores is the fraction of the accessible water which is most resistant to evaporation on account of the higher capillary potential (see e. g. *Baver* (1940)).

Besides the small size a slender body shape will favour the existence in the soil. This feature is typically developed in nematodes. Also the locomotory type is important. Hydrophilous organisms which move by irregular torsions and bendings of the body (like nematodes) require less space (and water) than those which swim freely in the water (e. g. certain rotifers). An excellent illustration of this is furnished by protozoa.

The most successful protozoan inhabitants of the soil are the small flagellates (generally less than 10 μ diameter) which are present almost everywhere. Next in importance come the amoebae which are larger, it is true, (upwards of 50 μ diam.) but which may to a large extent adapt the shape and diameter to that of the

pores and crevices in which they live. In addition they do not swim. The least important soil protozoa are the ciliates. In most soils only small species occur regularly (especially *Colpidium* and *Colpoda*) and only in small numbers. The larger species are present as cysts during the greater part of the time only to become active when water is present in greater amounts. In localities with much accessible water (e. g. the bog soil, see above) a much richer fauna of large ciliates, which do not occur normally in soil, is found.

The adaptation of size and shape of soil protozoa to the special environment is further accentuated by the fact that individuals living in the soil are generally smaller than individuals of the same species living in freshwater or kept in liquid media, the reduction being comparatively larger in big than in small species. A special adaptation is seen in certain ciliates which will often become amoeboid in the soil. Dwarfish individuals are also typical of other soil organisms, see e. g. *Boye Petersen* (1935) concerning algae. A detailed discussion of the biology of soil protozoa is given by *Koffman* (1934).

The power of surviving desiccations seems to be another important adaptation of the hydrophilous microorganisms normally occurring in the soil. As far as can be seen it is common to almost all members of the group, microflora and microfauna. In nematodes it is well developed in the typical soil species. Some preliminary experiments were carried out to analyse this resistance. Several indications are at hand that it is small in typical freshwater species (e. g. *Mononchus macrostoma*), while it is large in typical soil and moss species (*Plectus parvus* and *P. rhizophilus)*. However, my material is not sufficient to discuss the problem in detail as yet.

This power of surviving adverse conditions in an anabiotic state is, as far as can be decided, confined to the hydrophilous animals, where it is very important because their power of leaving unsuitable habitats by locomotion is very restricted in comparison with mites and collembola. Thus it enables them to remain in the very milieu where other factors, especially the food supply, is optimum and to resume activity almost instantaneously when the physical conditions become favourable again without having been forced to utilize their own synthesized protoplasm. In addition this state involves excellent potentialities for dispersal and subsequent conquest of new habitats — especially as a very large proportion of these animals are parthenogenetic or hermaphroditic or able to multiply in other ways from a single individual (bacteria, protozoa etc.).

The soil is an ever shifting biotope with regard to several biological and edaphic factors. Moss cushions are often still more inconstant in these respects. Water may be present as much larger bodies than in the soil but they are also much more liable to periodical desiccation.

The fauna of moss cushions is different from that of the soil in conformity

with this feature according to personal investigations. Mites and collembola are numerous here — they are able to leave the locality if conditions cannot be tolerated during periods of drought or inundation. The hydrophilous animals are abundant too even very large species of ciliates, tardigrades and rotifers, which are more numerous here than in the soil. They require large water bodies for normal activity, which are, in fact, offered by several moss cushions. Nematodes are numerous but not so numerous as in the mineral soil. This is probably connected with the fact that an effective utilization of the large surfaces requires a special locomotory mechanism which is possessed only by some species, which in consequence are very important in moss cushions.

In the extremely dry cushions e. g. on tree trunks *Plectus rhizophilus* (the most typical and common moss nematode) may be the sole species occurring. In less extreme localities other species are numerous. especially if a dense bottom layer is present, where conditions are more constant.

Of course, all the species living successfully in periodically dry moss cushions must possess the power of surviving periods of drought in an anabiotic state, which is, indeed, the case. Even the drought-resistant harpacticids of the genus *Moraria* may be extremely common in moss, while they are never found in normal soil.

For a discussion of the conditions of life in moss cushions and the fauna of this biotope see *Heinis* (1910), *Rahm* (1923, 1924) and *Overgaard* (1948 b).

Considerations similar to those of the preceding pages can also be attained by regarding the vertical distribution of hydrophilous (nematodes and harpacticids) and aerophilous microanimals (proturans) in the same locality.

These features are shown for the beach in fig 4 *a, c* and *e*. It is seen that nematodes are especially abundant 1. as near to the surface as the general conditions will allow them (cp. p. 53 ff) as an upper maximum and 2. 10—30 cm above the ground water, in the horizons where capillary water is present. The harpacticids require more water corresponding to their locomotory type (swimming) and larger size. Consequently they are especially numerous in and immediately above the ground water, their maximum being located lower than that of nematodes. 30 cm above the water table they have disappeared completely while nematodes occur right to the surface. The aerophilous proturans cannot live in surroundings with excessive water. Their maximum is located near the soil surface, nearer to it than the upper maximum of nematodes, while they have completely disappeared 25 cm below the surface, where 5 % water is present (it must be remembered that the soil consists of pure sand, thus this amount is not unimportant).

According to this discussion we may conclude that nematodes are primitively aquatic microanimals which are especially adapted to live in the pore spaces of

the soil. The adaptations are manifest in their small size and slender shape, their type of locomotion not requiring much room, and their power of anabiotic existence. In most soils they are probably constantly active, while in especially dry localities (e. g. the *Corynephorus* slopes and certain moss cushions) they must be inactive periodically. The size of most nematodes is so small that the pore size is probably insignificant in determining their distribution, at least the composition of the nematode fauna in horizontal and vertical directions does not show the correlation of size of animals and size of pores which was found by *Weis-Fogh* (1948) in mites and collembola of the Plain. In principle the aerophilous and hydrophilous microorganisms have distinctly different requirements, and they cannot be regarded an ecologically homogeneous group.

8. THE OXYGEN-CONSUMPTION OF NEMATODES

In the preceding chapters the qualitative distribution of the fauna has been discussed. However, the number of individuals per unit area (volume) does not give any picture of the activity of the fauna, and the statements of weight per unit area only do so if we are sure that the metabolic rate of the different species is of the same order.

Within so uniform a group it can be presumed that the food absorption is proportional to the respiratory metabolism irrespective of the species. Thus a knowledge of the 0_2-consumption should be very valuable for a discussion of the importance of nematodes in the organic transformations taking place in the soil. As no data were accessible in the literature I have carried out a systematic investigation of the problem in the most important species in the different size groups (technique see p. 16).

1. 0_2-consumption under standard conditions.

(Bottom-drop: pure tap water, 0_2-pressure $\sim$ conditions of the atmosphere, instantaneous absorption of CO_2, temperature 16° C $\pm$ 0°,01).

In table 20 the values of 0_2-consumption for some important soil nematodes are given in terms of cc 0_2 (reduced to 760 mm Hg-pressure and 0° C) per hour and per kg.

All the values have been calculated as an average of 5—22 single measurements except for *Dorylaimus regius* where only 1 measurement was at hand.

In fig. 7—9 three single experiments are reproduced from my journal in order to give an idea of the alteration of the equilibrium pressure in experiments on species of different weights.

The errors of the method cannot be stated generally, but they are estimated

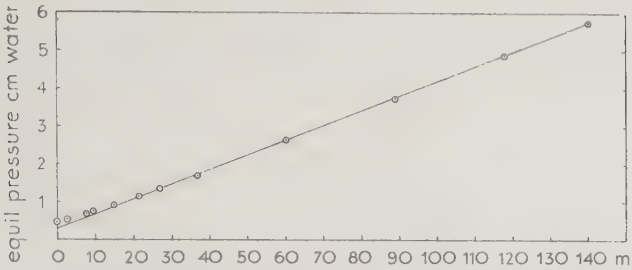

Fig. 7. An experiment of measuring the O_2-consumption of 11 adult ♀♀ of *Plectus cirratus*. The alteration of the equilibrium pressure per hour (Δ p) is ca. 24 mm water. From this value the O_2-consumption can be calculated, when the "diver constant" (v) is known (= the total gas volume of the diver floating in its equilibrium position at a known pressure and temperature) in this case it is 17.45 µl.

The O_2-consumption $= \Delta v = \frac{v \Delta p}{1000} \times \frac{273}{273 + t}$ where (273 + t) is the temperature (absolute) during the measurements. The graph representents an O_2-consumption of 1550 cc per kg per hour.

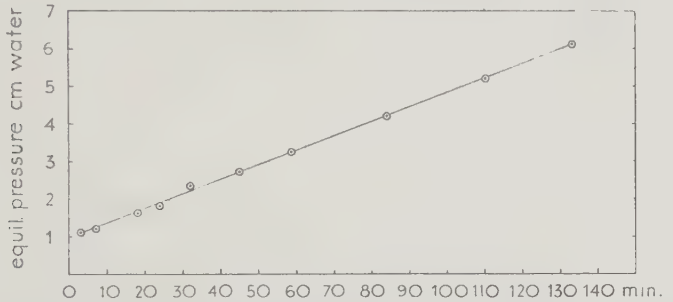

Fig. 8. An experiment on 1 ♀ of *Dorylaimus regius*. The effect (= alteration of the equilibrium pressure per hour) is ca. 23 mm i. e. of almost the same size as in fig. 7. Diver constant 17.75 µl. O_2-consumption 700 cc per kg per hour.

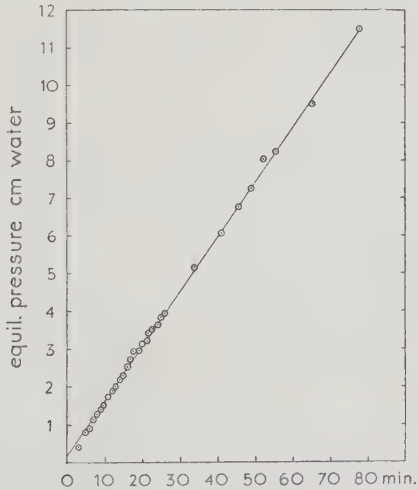

Fig. 9. An experiment on 1 ♀ juv. of *Pontonema vulgare*. The effect is in this case ca. 87 mm and the diver constant 16.95 µl. The O_2-consumption in this experiment was not calculated.

Table 20.

no.	average weight γ		O_2-consumption cc/kg/hour.
1	0.2	*Monhystera vulgaris*	1440
2	0.3	*Prismatolaimus dolichurus*	1400
3	0.5	*Plectus parvus*	1360
4	1.0	*Plectus rhizophilus*	1270
5	1.0	*Plectus granulosus*	1130
6	0.5	*Tylenchus filiformis*	1110
7	0.4	*Aphelenchoides parietinus*	1060
8	5.0	*Mononchus macrostoma*	1010
9	0.2	*Achromadora dubia*	1000
10	0.6	*Rhabditis monhystera*	970
11	3.0	*Tripyla setifera*	950
12	0.6	*Acrobeles ciliatus*	920
13	5.0	*Mononchus papillatus*	850
14	5.0	*Mononchus brachyurus*	850
15	2.0	*Dorylaimus carteri*	840
16	0.6	*Cephalobus persegnis*	810
17	0.8	*Cephalobus elongatus*	800
18	0.4	*Cephalobus nanus*	780
19	1.0	*Tylencholaimus mirabilis*	750
20	56.0	*Dorylaimus regius*	700
21	13.0	*Dorylaimus tritici*	675
22	10.0	*Dorylaimus obtusicaudatus*	670
23	0.7	*Rotylenchus robustus*	660
24	400.0	*Pontonema vulgare*	170

small by *Holter* (1943) and it is indeed obvious from fig. 7—9 that the method works satisfactorily in the case of nematodes too.

As is seen from the table and more directly from the accompanying diagram (fig. 10) the level of O_2-consumption is different in different species when adult specimens are compared.

As found by *Zeuthen* (1947) in marine invertebrates the respiratory rate tends to decrease with increasing size, although exceptions occur. For ecological purposes it is justifiable to establish the following groups with regard to oxygen consumption:

Monhystera, Prismatolaimus ..... using 1500 ± 200 cc O_2/kg/hour. at 16° C.
Plectus ..... — 1200 ± 200 cc —
Dorylaimus, Tylencholaimus, Tylenchus, Rotylenchus, Aphelenchoides, Mononchus, Cephalobus, Rhabditis, Tripyla, Achromadora, Acrobeles — 800 ± 300 cc —

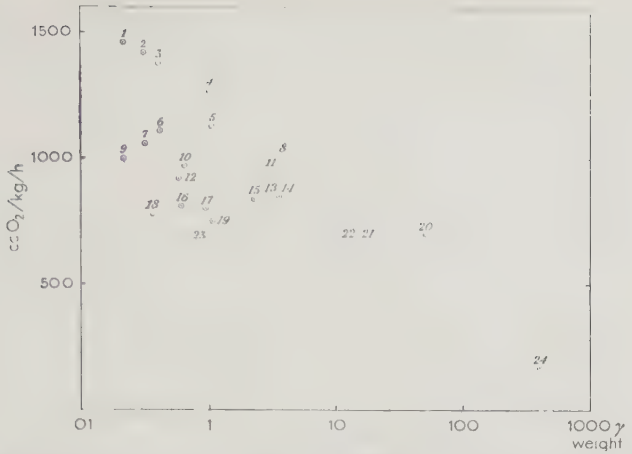

Fig. 10. Respiratory rate (at 16° C) of adult soil nematodes and the marine species *Pontonema vulgare* (24) in relation to the average weight of the species (logarithmic scale). Each point represents an average calculated from 5—22 experiments except in *Dorylaimus regius* (20) where only a single measurement was performed.

When comparing this survey with the general behaviour of the nematodes it is apparent, that *Monhystera*, *Prismatolaimus* and *Plectus* are very active animals, they are good swimmers and during the measurements they were moving about rapidly in the bottom drop, while other species e. g. *Dorylaimus*, *Tylencholaimus* were almost immobile.

Although in several species a direct correlation was seen between a high visible activity and a high metabolic rate the rule was found not to be universally valid, e. g. several species of *Rhabditis* and *Cephalobus* showed high activity but not a correspondingly high metabolic rate, and in the larger species (e. g. *Mononchus* and *Dorylaimus*) the difference between the metabolic rate of highly active and sluggish species was relatively insignificant.

Thus some indications were at hand that the mere external activity might influence the level of 0_2-consumption, a fact which would be important for the ecological utilization of the respiration measurements.

However, it turned out that matters had to be explained otherwise. If the locomotion was inhibited with urethane (0,9—1,5 %) it appeared that the 0_2-consumption was lowered ca. 5 % only. (The experiments were performed by measuring the consumption of normal individuals, after this they were pipetted out of the diver, narcotized and transferred to the same diver for another measurement where 1 % urethane served as bottom drop). In two cases a reduction exceeding 10 % was measured, namely in *Plectus cirratus* (15 %) and in *Mononchus papillatus* (20 %) (fig. 11), both species being very active and swimming freely in the water.

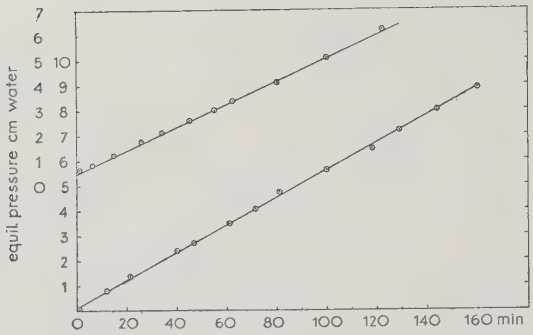

Fig. 11. Two experiments showing the influence of urethane upon O_2-consumption of *Mononchus papillatus* (5 ♀ ♀). Under standard conditions (below) the effect is ca. 33 mm. The O_2-consumption of the same five individuals in the same diver but narcotized with 1.5 % urethane (above) produced an effect of ca. 28 mm. Thus, as all other conditions were unaltered, the consumption is $100 \div \frac{2800}{35}$ = 20 % lower than in normal animals. This is the largest effect obtained in all my experiments (26).

Thus it is evident that rapid locomotion in nematodes is not the primary cause of a high metabolic rate but in several cases it may be considered an indicator of a high rate. It may be mentioned here that the urethane had to be 2—3 times as concentrated as that used for most other animals (*Krogh* (1914)). More dilute solutions had no effect at all, *Mononchus papillatus* being insensitive to the action of 0.8 % and *Plectus cirratus* to a 1.2 % urethane during 3 hours). Probably the question of activity is much more profoundly inherent in the tissues and not accessible to direct examination. My measurements on nematodes at all events justifies one in neglecting the influence of locomotion and extending the conclusion of *Zeuthen* (1947) to this animal group too: "the work of ... swimming of the micro-animals ... requires less than 50 %, in some cases perhaps only a negligible fraction, of the total energy production of the animals". This is quite logical, as the real work performed during swimming is very small.

2. Influence of O_2-tension.

When the changes in equilibrium pressure of the diver are known, it is possible to calculate the average oxygen tension of the diver during the experiments (cp. *Zeuthen* (1947)).

It is found that a change in equilibrium pressure of 10 cm corresponds to a change in O_2-tension in the diver of approximately 1 % of an atmosphere. The manometer used by me allowed one to measure changes of equilibrium pressures of about 100 cm ~ a decrease by 10 % of an atmosphere. Within these limits no differences at all in the O_2-consumption appeared. Experiments with this object in view were performed on *Plectus rhizophilus, Cephalobus persegnis, Rhabditis monhystera, Dorylaimus obtusicaudatus, Mononchus papillatus,* and in addition

on the marine species *Pontonema vulgare* and the vinegar eel *(Anguillula aceti)*. In no case was an effect found which could be ascribed to the decreasing O_2-tension, and thus it is probable as it was to be expected in these tiny animals that within the variations of O_2-tensions in normal soil the O_2-consumption of nematodes is independant of O_2-tension. Probably a much larger reduction of O_2-pressure might show an effect. This was, however, considered outside the purpose of this investigation. On a later occasion I hope to be able to carry out such measurements, as they are important for the understanding of the life conditions inside rotting potatoes, beets etc. in the soil. In such localities certain species of nematodes often abound.

3. Influence of food content.

In several animals it has been found, that the oxygen consumption is different in feeding and starving animals. It is important to know the influence of this factor especially in a quantitative investigation where many individuals are to be considered and where all nutritional phases may be present (as is the case almost everywhere except in homogeneous cultures).

Two opposite possibilities arise: the presence of food in the gut either influences the O_2-consumption significantly or the factor may be neglected; in each of the two cases different average values of metabolic rate must be estimated when considering the populations of natural localities.

To elucidate this problem in nematodes the following experiments were performed: On four successive days the O_2-consumption of the following individuals were measured: 2 *Dorylaimus obtusicaudatus* ♀♀ add., 4 *Mononchus papillatus* ♀♀ add., 20 *Plectus granulosus* ♀♀ add. and 1 *Pontonema vulgare* ♂ ad. and

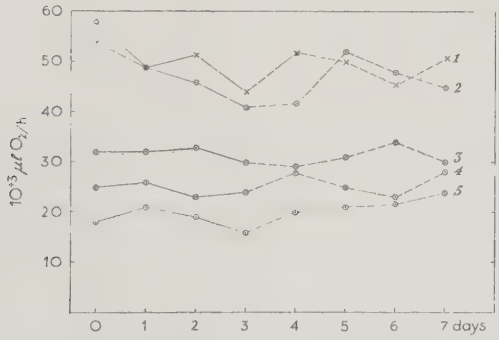

Fig. 12. Influence of nutritional condition upon the O_2-consumption in 1. *Pontonema vulgare* 1 ♀ ad., 2. *P. vulgare* 1 ♂ ad., 3. *Mononchus papillatus* 5 ♀♀ add., 4. *Plectus granulosus* 20 ♀♀ add. and 5. *Dorylaimus obtusicaudatus* 2 ♀♀ add. Measurements were performed each day on the same individuals during three days with ample food supply (full line) and during four days of starvation broken line). The O_2-consumption is expressed in $10 \div^3$ µl per hour in each of the five cases.

1 *Pontonema vulgare* ♀ ad. All the individuals were kept in surroundings with plenty of food and after each measurement they were transferred to the same substratum. From the fourth to the seventh day they were kept in sterile tap water, *Pontonema* in sterile artificial sea-water (30 ‰).

In the diagram fig. 12 the results have been given. No indication is seen of a fixed tendency, all the values are placed in a rather haphazard way within the natural limits of reproducibility of the measurements. Consequently it was concluded that in a natural population there is no reason to believe that a difference in the state of nutrition of the single individuals will introduce any significant error into the material.

4. Influence of age and sex.

In the estimation of the importance of these factors, certain difficulties are met with namely that the immature stages of the experimental animals are so small, that a great number is necessary for obtaining reliable measurements, and on account of the impossibility of measuring the volume of the individuals in an active state these measurements cannot be made until after the diver experiments, so it was impossible for me to procure enough individuals of an identical size for the experiments.

Another procedure was followed: *Zeuthen* (1947) concludes that the metabolic rate of a certain species decreases as the body size increases, and that the decrease in oxygen consumption is especially steep when the species approaches its maximum size, "in other words, as growth (maybe due to genetical or endocrine factors) gradually ceases". The fact was demonstrated by *Zeuthen* in several marine animals. On account of the small size of the experimental animals it could not be proved directly in soil nematodes. However, it is a very important question in ecology. Consequently it may be worth mentioning that I was able to confirm the rule in a representative of the marine nematodes (not especially studied by *Zeuthen)*, and in a soil animal.

The only species of nematode accessible to me which allowed such measurements with my technique was the marine species *Pontonema vulgare* (originating from Isefjord, Sealand). In fig. 13 all the measurements are expressed diagrammatically; it must be pointed out that in the case of juvenile and adult individuals of approximately the same size the juvenile ones show the highest metabolic rate. In the case of adult individuals of rather different size, the oxygen consumption is practically identical irrespective of sex and reproductive phase, adult ♂♂, adult ♀♀ with and without eggs do not deviate essentially from this common value. For certain nematodes at least it may thus be concluded that, in quite young individuals the metabolic rate is high, during growth and maturation a

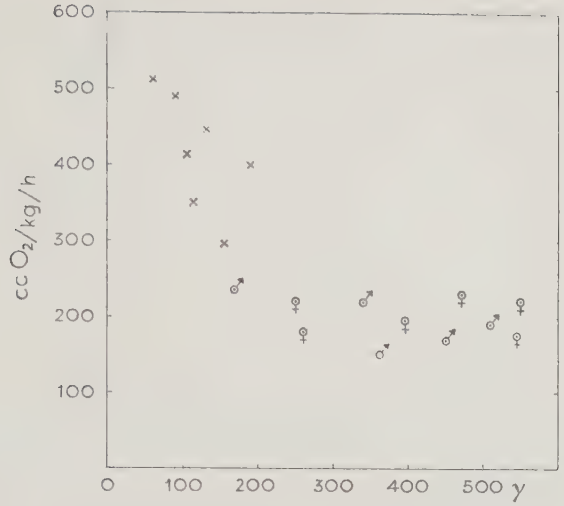

Fig. 13. Weight and respiratory rate in *Pontonema vulgare*. × indicates immature individuals, ♀ and ♂ adult females and males respectively.

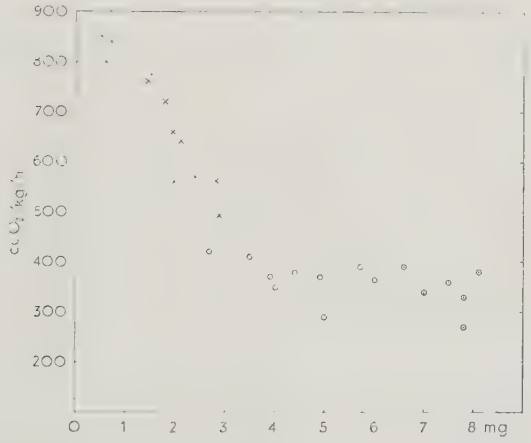

Fig. 14. Weight and respiratory rate in *Mesenchytraeus albidus*. × indicates immature and ⊙ adult individuals. Weights found by weighing.

pronounced decrease is present. When entering the last moult the oxygen consumption has reached a certain, lower, value where it seems to be maintained until the death of the animal. (In nematodes the presence of an external opening of the genitalia furnishes a test that the individuals have reached the adult stage).

As a representative of the soil fauna *Mesenchytræus albidus* was chosen. In fig. 14 the measurements are expressed in the same way. An identical tendency is evident. However, it cannot be stated generally that all immature individuals

are to be found on the decreasing part of the curve because in this species we have no practical test of maturity which could be applied for my purpose. Conversely it cannot be satisfactorily shown that all measurements on the horizontal part of the curve were performed on adult individuals. The only indication which can be given is that no individual weighing less than 2.7 mg had a clitellum. However, the identity of the curves in the two species seems to allow the general conclusion that in certain soil animals young individuals have a higher metabolic rate than adult individuals of the same species.

This makes it justifiable to believe that the rule is of rather general validity. However, it may be stressed, that growth is not necessarily the factor which evokes the phenomenon. As is indicated from the two diagrams ,and later on it was proved by way of culture, growth does not at all stop when the oxygen consumption has reached a constant level. Thus it seems probable that the operating factor is some sort of biochemical maturation process, as the metabolic rate becomes constant when sexual maturity is attained.

5. Influence of temperature.

Apart from the age of the experimental animals temperature is probably the factor which causes the most profound alterations in the respiratory rate in nematodes. This conclusion was obtained from two series of experiments carried out with *Mononchus papillatus.*

A large portion of moss (*Hylocomium parietinum* and *Stereodon cupressiformis*) containing a dense population of this species was collected in Högildgaard Plantation on 27. Dec. 1947, and stored at 9° C. From this material individuals were taken for measurements, which were begun on 20. Jan. 1948.

When the animals were transferred directly from the moss to the divers and measurements were started immediately, irregular values were obtained during ca. one hour. After this period respiration was very regular during the measuring period of 2—4 hours. In some cases another measuring period was used 7—12 hours after the first one and in all cases a third one about 20—24 hours after the beginning of the experiment. All the measuring periods lasted for 2—4 hours. The 4—6 individuals of *Mononchus papillatus* used for each experiment were thus transferred from 9° C to the divers and subsequently into the flotation vessels, the temperature of which had been adjusted beforehand to a certain value. After 1 hour's delay measurements were begun. The values of metabolic rate obtained in this way are given in fig. 15.

Thus it was verified that at least in this species of soil nematodes it is justifiable to estimate the oxygen consumption at different temperatures on the basis of the curve obtained. Some preliminary measurements on *Plectus cirratus* lead to the same conclusion, which probably applies to all soil nematodes. The experiments on this and other physiological problems are to be continued.

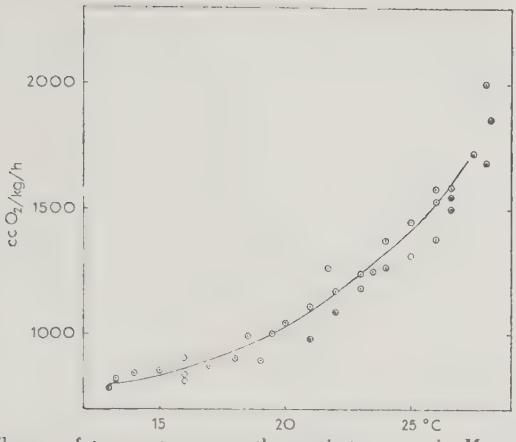

Fig. 15. Influence of temperature upon the respiratory rate in *Mononchus papillatus*.

This temperature-respiration curve corresponds nearly to that compiled by *Krogh* (1914) bearing upon cold-blooded vertebrates. *Ellinger's* measurements (1916) upon *Culex annulatus* could also be expressed by means of this curve, and for ecological purposes it has been used by *Bornebusch* (1930).

A question which has been discussed several times is that of the physiological temperature adaptations of animals transferred from one to another temperature. In short range experiments they will as a rule be in accordance with the standard metabolism curve of *Krogh*, while in long range experiments secondary adaptations will often occur (see *Zeuthen* (1947)).

In soil nematodes it was not possible to demonstrate such secondary adaptations. *Mononchus papillatus* was kept during four months at the temperatures 2, 9, 16 and ca. 21° C. When individuals from each of these temperatures were transferred to divers and the 0_2-consumption was measured at 16° C. it was not possible to find systematic deviations from a mean value correlated with the different temperatures at which the animals were kept. Thus the temperature adaptation is rapid, a fact which is also confirmed by measurements on individuals of *Plectus granulosus* taken from a natural locality throughout a year.

Several problems are met with in connection with the temperature-metabolism relation at higher temperatures. For ecological purposes they are without greater importance. In a subsequent paper the problems of this section will be treated in further detail.

6. Ecological employment of the oxygen consumption.

The 0_2-consumption is an important ecological tool. When systematically related animals of similar and known nutritional biology are compared, such measurements allow us to draw certain conclusions as to the activity and importance of the species in question.

Of course, they will only give approximations. However, such values are often very important because it may be extremely difficult to get any idea of the quantity of food consumed in the natural environment.

In the case of nematodes the values given in table 20 may be employed for a calculation of the oxygen consumption per unit area of the soil when the exact qualitative and quantitative composition of the fauna is known. However, I have found the rough values p. 68 to be sufficient for the purpose because only orders of size are aimed at. The percentage of young individuals of different sizes could not be taken into consideration as it would involve a measurement of each individual found, which was, of course, impossible. Another error was introduced because the respiratory rate is not known in all species, only in the more important ones. The respiratory rate of these species has been fixed by analogy with known species of the same genus or similar size and locomotory activity.

A calculation of the oxygen consumption at an annual mean temperature according to the temperature-metabolism curves was not performed because the temperature records of the Mols Laboratory did not allow the calculation of a reliable annual mean temperature. Thus only a temperature of 16° C has been employed.

9. THE NUTRITION OF FREELIVING NEMATODES WITH NOTES ON MORPHOLOGY AND REPRODUCTION

1. Review of literature.

The nutrition of freeliving nematodes has been touched upon by several authors partly as stray observations pertaining to the feeding biology of single species or genera and partly as general considerations on the whole group.

It is impossible to review the entire literature on this problem, as it is scattered all over the nematode literature. However, some of the more important references are given here.

Bastian (1865) supposes that the freeliving nematodes almost exclusively feed on material of plant origin. However, in some freshwater species (e. g. *Cyatholaimus* and *Spilophora)* he found diatoms and algae in the gut. He believes the food to be ingested by sucking.

De Man (1884) is of opinion that the food of nematodes is of plant origin except for *Dorylaimus spp.* (he observed a *Dorylaimus sp.* which had pierced the cuticle of a *Cephalobus sp.* by its stylet). Also *Mononchus sp.* may feed on animals (in one case a *Dorylaimus sp.*). *Oerley* (1886) states that the freeliving Rhabditids feed on decaying materials of plant and animal origin. *Diem* (1903) finds nematodes to be especially abundant near plant roots and supposes accordingly that

they generally feed on "frischen oder lebenden pflanzlichen Stoffen, wie manche Kulturschädlinge ihrer Familie". *Marcinowski* (1906, 1909) comes to the conclusion that the "semiparasites (i. e. *Cephalobus*, *Rhabditis*, *Plectus* etc.) are polyphagous "indem sie nicht nur keine Gebundenheit an bestimmte Wirtspflanzen zeigen, sondern auch von anderer als pflanzlicher Nahrung zu leben vermögen z. B. von faulem Fleisch". *Hofmänner* (1913) finds diatoms in the gut of *Theristus setosus*. *Potts* (1910) believes that *Rhabditis* and *Diplogaster* generally feed on decaying substances of plant and animal origin. However, they can be reared in cultures of bacteria and are able to feed on bacteria or their products. The species having a stylet (*Tylenchus, Dorylaimus* etc.) feed on plant juices. *Francé* (1921) has: "Ebensowenig zweifelhaft ist es, dass Rotatorien und Nematoden nebst Humusstoffen auch Mikroorganismen aufnehmen, obwohl es mir wenigstens in bezuf auf die letzteren nicht gelang, eigene Angaben beizubringen". *Menzel* (1914) states that *Aphelenchoides parietinus* may feed on the alga *Chlamydomonas nivalis* which diet causes a red coloration of the gut. *Heinis* (1916) mentions that he has seen a *Dorylaimus sp.* in an empty test of *Nebela collaris*; the fact is interpreted by assuming that the nematode has eaten the rhizopod and taken over its test (for protection?). In another case he saw a *Dorylaimus sp.* attacking and devouring a rhizopod. *Steiner (1916)* states the food of *Rhabditis marina* to be bacteria and unicellular organisms e. g. flagellates. The food of the *Dorylaimus* species (1917) consists of plant juices which they procure by piercing the tissue and applying suction. The gut is often green from chlorophyll. The soil species may attack roots, but he believes that they do not avoid tissue juice of animal origin. *Steiner* and *Heinly* (1922) give the following summary of the nutrition of nematodes: "There have been no very comprehensive studies made of this question up to the present, and our knowledge is based mostly on occasional observations. The results of these show that some forms such as *Rhabditis, Cephalobus* etc. feed on decaying matter, that is on the contained bacteria or bacterial products; others, such as *Tylenchus, Heterodera, Aphelenchus* etc. feed on plant tissues or fluids; others such as *Dorylaimus* etc. feed probably on both plants and animals; and still others such as *Mononchus papillatus,* described in this paper, are apparently exclusively predatory". Later on they state that nematodes play a very important role "as a factor in the humification of the soil, in transformation and removal of all kinds of organic matter, decaying bodies, etc.". *Cephalobus subelongatus* Cobb may be reared in "a drop of water containing parts of grains, leaves and stalks of corn (*Zea mays*); various other plant materials were also used with success. *Cobb* succeeded in rearing *subelongatus* in macerated silage; in this case cockroach meat was also used, both foods being productive of good results". From this *Steiner* (1925) concludes: "*Subelongatus* may therefore be regarded as omnivorous and well fitted for varied life conditions". Discussing *Dorylaimus regius* he

writes: "In estimating the economic significance of soil nemas, a knowledge of their food and feeding habits, of which very little is konwn, is of chief importance. There are two ways to determine the food of these nemas, (1) by experimental feeding, (2) by a study of the intestinal contents. The first is difficult on account of the environment—the soil; the second, because the sucking way in which most forms feed renders the intestinal contents more or less unrecognizable; nevertheless, knowledge important to the study of soil economy can be gained by careful study of the intestinal contents. Such a study of the four specimens of *Dorylaimus regius* resulted in finding an oligochaete seta ... Therefore *D. regius* undoubtedly ingests animal matter". *Steiner* (1928) writes: "This form (*Plectus granulosus*) has already been claimed by several authors as feeding, at least partly, in plants. It has been mentioned from seedlings of cereals and *Micoletzky* (1921) found chlorophyll as intestinal content". And on *P. communis*: "This form seems to live, at least partly, on fungus mycelium. A. partly digested mycelial thread was distinctly seen in the intestine".

Menzel (1920) reaches the following conclusions: *Mononchus spp.* feed on nematodes, rotifers and oligochaeta, *Tripyla papillata* on nematodes, rotifers and tardigrades and *Trilobus gracilis* on rotifers. The results were obtained by investigating the gut contents and by culture experiments. Apart from these reliable analyses he supposes without proving it that all species with a bulbus oesophagi (*Rhabditis, Diplogaster, Cephalobus, Plectus* etc.) ingest liquid food only, while the genera without a bulb are predators (*Mononchus, Tripyla, Ironus* and many marine species). *Dorylaimus* and all the *Tylenchinae* feed on juices of plant and animal origin, which they suck by means of the stylet.

Micoletzky (1921) agrees that *Mononchus* and *Tripyla papillata* generally feed on other animals, however, universally valid statements cannot be made as he has found *T. papillata* feeding exclusively on diatoms in the Lunzer lakes. Also *Ironus* and *Trilobus* feed mostly on animals. *Dorylaimus, Tylenchus* and *Aphelenchus* "scheinen vielfach frische Pflanzengewebe vorzuziehen". They live as parasites or semiparasites on plant roots. However, *Dorylaimus flavomaculatus* may attack chlorophyll containing parts of *Hypnum sp.* Several (*Cephalobus, Rhabditis* and others without a stylet) "ernähren sich von in Zersetzung befindlichen Pflanzen- und Tiergeweben, bewohnen daher meist sehr humöse oder fäulnisreiche Erde, bzw. zeigen den Höhepunkt ihrer Entfaltung im Herbste, zur Zeit des grossen Pflanzensterbens".

Micoletzky (1925) has: "Im Allgemeinen haben wir zwischen Pflanzenfressern, Tierfressern und Mulm- oder Detritusfressern zu unterscheiden. Die Pflanzenfresser zerfallen wieder in Verzehrer lebender Pflanzensubstanz und in solche, die sich von abgestorbenen Pflanzen ernähren. Erstere lassen sich in Algenfresser und Sauger von Pflanzensäften einteilen". According to this author all species having a stylet

live parasitic on plants, however, some of them (*Dorylaimus filiformis, D. flavomaculatus, Aphelenchoides parietinus*, now and then also *Tylenchus*) may in addition suck algae, "worauf das ständige Auftreten gewisser stacheltragender Arten in ausgesprochener Algenumgebung mit ziemlicher Bestimmtheit hindeutet". ... "Zwischen den ausgesprochenen Pflanzen- und Tierfressern stehen die Detritus- oder Mulmfresser, zu denen eine grössere Zahl von Nematoden, namentlich aus Moos und Moor, gehören" ... "Die Konservierung des Detritus durch Humussäuren weist darauf hin, dass ein grosser Teil der Moorbewohner zu den ausgesprochenen Humusfressern zahlt, so *Teratocephalus*, *Prismatolaimus* und ins Moor stark hervortretende Arten von *Plectus*. Im übrigen finden wir gerade bei *Plectus* und *Cephalobus* mehrfach Übergange zur Ernährung durch verwesende Stoffe, die für *Rhabditis* und *Diplogaster* zur Regel geworden ist, wobei pflanzliches und tierisches Gewebe in verschiedener Weise von den einzelnen Arten bevorzugt wird".

It is a well known fact that several parasitic nematodes spend the larval stages free in the soil. This is the case in *Ancylostomum caninum* which spends the two first larval stages in faeces from dogs on the soil surface. During this period the larva feeds actively, two ecdyses occur and the length is doubled. *Loos* (1911) came to the following conclusion with regard to the nutrition of the freeliving larva: The normal food of *Ankylostomum* larvae constists of the finest solid constituents of the feces, perhaps also of certain substances contained in them in solution". Later on he states that "bacteria have not a sufficient nutritive value for the larvae". *McCoy* (1929) studied the same problem in the same species. For this very nice investigation he obtained sterile eggs from the feces, transferred them to agar plate cultures of different bacteria, where the larvae hatched normally and reached the infective stage in about 7 days on bacteria as sole food. In normal suspensions of bacteria in salt solutions they would also reach the infective stage. On heat killed bacteria and sterile filtrates of salt suspensions normal development did not occur. *McCoy* cultivated the larvae successfully on the following bacteria (retaining the original nomenclature): *Bacterium coli, B. lactis aerogenes, B. alcaligenes, B. cloacae, B. pneumoniae, B. mycoides corallinus, Proteus vulgaris, Erythrobacillus prodigiosus, Spirillum rubrum, Vibrio Metchnikovi, Bacillus cereus, B. megatherium, B. pseudotetanicus, B. subtilis, Micrococcus citreus, Staphylococcus aureus, St. album, Sarcina alba, Streptococcus pyogenes, Str. viridans, Str. haemolyticus* and *Micrococcus ovalis*. They could not be reared on *Bacillus pyocyaneus, B. mycoides* and *Sarcina lutea*. A single experiment with the yeast *Torula rosea* was negative. He concludes: "The sum total of the evidence from the experiments indicates that living bacteria are the essential food utilised by hook-worm larvae in developing to the infective stage".

Schneider (1939) gives the following information on the nutrition of freeliving nematodes: "Soweit etwas darüber bekannt ist, sind die freilebenden Fadenwürmer

in der Mehrzahl Pflanzen- oder Detritusfresser, zum kleineren Teil führen sie eine räuberische Lebensweise".

Hempelmann (1932) summarizes: "Die Nahrung der Nematoden ist wohl meist eine flüssige, indem diese Würmer einfach das feuchte Medium, in dem sie leben, aufsaugen und durch ihre Darm passieren lassen. Meist besteht die Nahrung aus organischen Säften".

Lapage (1937): Many free-living nematodes of to-day eat algae, diatoms, bacteria and fungi and some of them are predatory, devouring rotifers, tardigrades and other nematodes (*Mononchus*, *Trilobus*). Other free-living nematodes seek environments rich in dissolved organic substances, such as manure and decaying plant and animal material, in which they live a saprozoic life. Those who have studied them are not, however, agreed about their diet".

Filipjev and *Schuurmans Stekhoven* (1941) distinguish three groups, 1. plant parasites *(Tylenchidae)*, 2. those using decaying organic matter as a substratum *(Rhabditis, Diplogaster, Cephalobus* etc. and perhaps also *Monhystera)* "Many of these species do not eat the putrefying vegetable or animal material itself, but the bacteria, which live upon the same material and can be reared not without great difficulty in sterile media... Decaying plant material affords favourable conditions to the development of quite a fauna of saprozoitic nemas, among which species of *Cephalobus* and *Acrobeles* form the bulk." A third group comprises the predators.

Stöckli (1943) distinguishes four ecological groups of nematodes: 1. omnivorous, 2. carnivorous, 3. nekrobiontic and 4. saprobiontic species. The freeliving omnivorous species feed on dead and living organic matter: fungus hyphae and spores, algae, bacteria, protozoa, rotifers, tardigrades, nematodes, oligochaeta, larvae, eggs, insects and also dead organic matter and plant and animal secreta may serve as food. To this group belong the *Dorylaiminae*. "Die nicht stacheltragenden Dorylaiminen findet man vorzugsweise in faulenden Planzenteilen. Doch spielen sie nur eine sekundäre Rolle, indem sie vollenden, was andere begonnen haben."

Lyon and *Buckman* (1943): "Three groups of nematodes may be distinguished on the basis of their food demands: (1) those that live on decaying organic matter, (2) those that are predatory on other nematodes, small earthworms, and the like, and (3) those that are parasitic, attacking the roots of higher plants, passing at least part of their life cycle embedded in such tissue. The first group is by far the most numerous in the average soil and most varied."

As it appears from the above review of some of the extremely scattered literature no generally accepted conclusion has been obtained regarding the nutrition of the freeliving nematodes of the soil. The question has been touched upon by most authors working on nematodes,

however, generalisations on the basis of a few occasional observations have created an enormous confusion. The information given in the ordinary textbooks and manuals of zoology and soil biology is contradictory to the same extent, but probably the most usual concept is the one held by *Lyon* and *Buckman* (1. c.), which is quoted to serve as an example.

Applying the criterion that no conclusion is considered reliable unless it was reached by way of experiment or large-scale direct observation the following summary is obtained:

1. A group among the soil nematodes are true plant parasites, living in constant association with plant roots. This is the case in *Tylenchulus* and *Heterodera*, where also morphological specializations are found. They are universally admitted to be severe pests in cultivated plants; in addition the fact has been confirmed by cultivation on plants roots in sterile media. For *Heterodera radicicola* see *Byars* (1914).

2. Another group of nematodes includes more or less typical plant parasites. Morphological modifications according to the parasitic habit are absent, however, the species in question often cause great damage to crops by attacking the roots. This applies to several species among which may be mentioned *Rotylenchus similis, Pratylenchus pratensis, Ditylenchus dipsaci, D. radicicola, Anguina tritici, Aphelenchoides olesistus, A, fragariae* and *A. ritzemabosi.* While the first group consisted of obligate parasites, of higher plants, this seems not to be the case in this group. *Christie* and *Crossman* (1936) were able to cultivate *Aphelenchoides fragariae* on certain fungi on agar plates in the absence of bacteria, and *Steiner* (1936) kept *Aphelenchoides limberi* on cultures of *Monilia sitophila.*

3. A large group comprising several *Tylenchinae* have often been found associated with plant roots and secondary damage of roots. However, the species are also found widespread in the soil in such a way that there is no reason to presume a very close association with plant roots. This applies among others to *Rotylenchus robustus, Tylenchorhynchus dubius, Tylenchus filiformis, Ditylenchus intermedius, Ecphyadophora tenuissima* and *Paraphelenchus pseudoparietinus.* However, the groups 2 and 3 are not sharply delimited and certain species (e. g. *Tylenchus davainei, Aphelenchus avenae* and *Aphelenchoides parietinus)* have been recorded as true plant parasites as well as freeliving species at least partly feeding on other things than the roots of higher plants. Several species are able to suck fungi (hyphae) but the importance of this food source is not known with certainty. *Aphelenchoides parietinus* may feed at least partly on *Chlamydomonas nivalis.* Much work is still to be done on the *Tylenchinae* to clear up the several obscure points. An especially interesting problem is the presence of more or less host specific strains within the same species (e. g. *Ditylenchus dipsaci).*

4. Nothing definitely can be said of the nutrition of the *Dorylaiminae.* Several

occasional observations are at hand, but they do not allow one to construct a general concept.

5. The genera *Mononchus, Tripyla, Ironus* and several marine genera feed mainly as predators on larger animals e. g. nematodes.

6. The species of *Rhabditis* feed on bacteria. Evidence of this has been furnished through the culture experiments of several authors. Especially *Dotterweich* (1938), *Ludwig* (1938) and *Hilgermann* and *Weissenberg* (1918) have elaborated special techniques for the culture of *Rhabditis* (especially *Rh. teres*) on plate cultures of bacteria. The concepts of these authors seem perfectly reliable even if *Collier* (1928) suggests that the nematodes do not feed on the bacteria, but the activities of the bacteria make it possible for the nematodes to absorb the partially decayed agar.

2. Personal investigations.

My own conclusions were obtained on the basis of examination of the gut contents of a very large number of individuals. The exact number cannot be stated but it constitutes more than half of my total material.

The direct observation of the gut contents is a difficult procedure on account of the smale size of the animals, and unless the method is applied to a very large material the results obtained are of restricted value because one single observation of a certain substance in the gut contents cannot decide whether it is a normal food substance or an occasional contamination. On the other hand, if the same substance is found repeatedly the probability increases, that it is part of normal food. However, it must be kept in mind that the recognizable substances left in the gut may remain there in such a state because they cannot be digested.

On the basis of this type of investigation it could be decided with certainty that none of the nematodes which I have found in the soil feed on humus in the same sense as do several insect larvae, *Enchytraeidae* and *Lumbricidae*. *Micoletzky* (1925) and several others advocate the theory of humus nutrition in freeliving nematodes such as *Plectus, Teratocephalus* and *Prismatolaimus*. However, humus is never seen in the gut of any nematode in the quantities necessary for maintaining life exclusively on this basis. All other real humus eaters have the gut completely filled with humus, and I believe these large quantities of ingested matter are necessary because only a very small fraction of it can be digested. When this seems to apply in the *Enchytraeidae* and *Lumbricidae* it should be probable to a still larger extent in nematodes where the metabolic rate is 5—10 times as high as in the former groups. In nematodes single particles of humus may be found in the gut in rare cases, especially in the larger species, *Mononchus, Tripyla* and sometimes *Plectus*. That the presence of single humus particles in the gut of these species is really ac-

Table 21.

no.		colour	Gram staining	source
1	short rod	white	÷	soil
2	short rod	greyish	÷	aquarium
3	long rod	white	÷	litter
4	large ovoid rod	white	÷	soil
5	mixed			root nodules, *Trifolium*
6	*Micrococcus sp.*	red	÷	soil
7	*Micrococcus sp.*	red	÷	soil
8	*Micrococcus sp.*	yellow	÷	soil
9	*Micrococcus sp.*	orange	+	?
10	*Sarcina sp.*	yellow	+	soil
11	"Streptococcus"	grey	+	soil
12	ovoid rod	red	÷	old bread
13	rod	grey	÷	potato
14	rod	grey	÷	feces
15	*Bac. mycoides*	white	+	soil
16	rod	white	+	hay infusion
17	*Leptothrix ochracea*			water reservoir
18	*Actinomycetes sp.*	brown		potato
19	*Cryptococcus sp.*	red		soil

cidental seems to be supported by the fact that *Mononchus* is a genus which has never been claimed to feed on humus, on the contrary all authors agree that it is a predator.

It may be stressed here that all the statements apply to soil biotopes. In the sea and in freshwater nutrition may be different even in species also occurring in the soil. Thus I have seen *Dorylaimus stagnalis* from freshwater biotopes, in this case the gut was invariably filled with a dark substance which could not be identified with certainty, but it reminded one very much of fine detritus.

The remaining problems of feeding biology were studied separately in the single species. In the following a survey of the results is given. As bacteria were found to be important in this respect I have made culture experiments with different species of bacteria serving as food. A few of the bacteria were identified, in most of them, however, this was not the case. For further details I refer to table 21, and to the technique described on p. 18.

Alaimus primitivus. Bacteria were demonstrated in the gut of more than 200 individuals, they could be stained in the oesophagus with methylene blue and erythrosin. In 23 specimens from the turnip field (table 9) a colourless yeast was found in great number.

The species could be reared and egg production induced in suspensions of *Micrococcus* no. 6. The larvae hatched normally and the adult stage was attained.

Tylencholaimus mirabilis. In most specimens from the *Corynephorus* slopes (table 5) chlorophyll was present in the gut. As the animals live in 5—10 cm depth it cannot originate from higher plants. Probably algae are the source. The species could be maintained on water cultures of an unknown algae for 6 weeks. During this interval 10 ♀♀ produced 3 eggs. This egg production appears to be very low, however, I cannot decide whether it is normal. In a suspension of unknown bacteria the animals died within 6 days.

Dorylaimus spp. In all species of this genus the occurrence of chlorophyll in the gut is normal. As in *Tylencholaimus* I believe that in nature it mostly originates from algae, other sources are difficult to imagine when the animals occur in depths upwards of 20 cm and I have never found species of *Dorylaimus* aggregated in leaf sheaths of grasses where the chorophyll might be easily obtained. Probably this genus is the most difficult one in which to analyse the food requirements. *Dorylaimus carteri* was maintained for 22 days in water cultures of *Hormidium flaccidum* + bacteria, however, the 13 ♀♀ produced no eggs. 24 ♀♀ kept in suspensions of bacteria (nos. 4—8, 10, 11, 13, 14, 15 and 16 and another unknown species) died within 5 days, and uterine eggs were not even laid. Fresh leaves of moss in water allowed the maintenance of 15 ♀♀ for 18 days but only two eggs were laid (present as uterine eggs at the transfer). *Dorylaimus obtusicaudatus* could be maintained in water cultures of *Hormidium flaccidum* + bacteria for 33 days, during this time 12 ♀♀ laid 7 eggs (5 were present as uterine eggs at the transfer). With fresh moss leaves as a substratum 9 females could be maintained for 33 days (3 eggs were deposited). In suspensions of bacteria (1—18 except 12 and 17) all the individuals died within 9 days. When dead, unsterile enchytraeids served as a medium, the animals died within 5 days. *Dorylaimus tritici* could not be maintained on *Hormidium* + bacteria or moss leaves (all died within 10 days). In suspensions of *Micrococcus* no. 6 and *Bac. cereus mycoides* death ensued in 3 days, while 6 ♀♀ laid 5 eggs when kept on dead unsterile enchytraeids for 20 days. In a sterilised soil suspension 3 ♀♀ (washed repeatedly in sterile water) died within 5 days. In sterile water death ensued in 6 days.

On the basis of these highly contradictory observations and experiments it is not possible to decide what is the basic nutrition of the *Dorylaimus* species. My original point of view *(Overgaard* (1948 b)) that soil algae play an important role is not invalidated, on the other hand it has not been proved by experiment until it is ascertained that the extremely low reproductive rate obtained in cultures of algae is of the same order as in the natural environment. It has not been possible for me to obtain any idea of this, consequently I prefer to maintain my original concept on purely logical reasons until evidence favours another supposition.

However, the point of view is only applied to certain species of *Dorylaimus* especially *D. carteri* and *D. obtusicaudatus*.

Tripyla setifera. Generally no recognizable gut content is seen in this species (or in *T. papillata*). Now and then single bacteria can be found in the oesophagus. One of my early experiments proved that the species could be reared in a hay infusion containing bacteria and ciliates (at a pH of ca. 4) Indications were at hand that it fed on the ciliates. Later experiments have shown that the species can be maintained at least 24 days (in sterile water they died in 4 days), in suspensions of bacteria (*Micrococcus* no. 6), however, mature and fertilized ♀♀ never produced a single egg, although large ovarial eggs were present. Thus it seems certain that the ciliates of the former experiment were utilized as food. In this case eggs were laid, which hatched normally, and the larvae reached the adult stage.

In comparing the statements of previous authors (*Menzel* (1920), *Micoletzky* (1921)) with my results it may be concluded, that the *Tripyla* species (*T. papillata* and *T. setifera*) feed on other organisms, among which nematodes, rotifers, tardigrades, ciliates (and probably other protozoa as well) and diatoms may be mentioned. Bacteria are not sufficient nutrition, as reproduction comes to a stop, however, as an accessory or temporary nutrition they may be valuable.

Prismatolaimus dolichurus. Bacteria may be found in the gut, but they are not of universal occurrence. Apart from bacteria I have never seen any recognizable contents. Often the gut contents show a dark coloration. On closer examination I have never been able to find dark particles in the gut, and the coloration seems to be diffuse.

In bacterial suspensions hatching, growth and reproduction is good when *Micrococcus* (no. 6—9), no. 16 or *Actinomyces spp.* were used as food. On *Sarcina sp.* and *Bacillus mycoides* death ensued in 6 and 8 days respectively probably because *Sarcina* grows in massive packages too large to be swallowed, the same applies to *B. mycoides* which forms thick strands, and on "*Streptococcus*" no. 11 in 10 days, each experiment comprising 5 individuals. In sterile water the animals died in 10 days.

Thus it cannot be doubted that the species is able to live on certain bacteria as food. However, the dark coloration of the gut was not seen in the experimental animals.

Mononchus papillatus. The universally accepted point of view that the species of *Mononchus* mainly feed on other animals was confirmed by me both by way of direct observation and experiment.

In a previous paper (*Overgaard* (1948 b)) I have recorded that young individuals of this species may feed on a *Coccomyxa sp.* in nature (the same is true of *Dorylaimus obtusicaudatus*). Later experiments have shown, that it can be

maintained on bacteria (*Micrococcus* no. 6) for at least 29 days. However, ♀♀ did not produce any eggs during this period.

Achromadora dubia. This species can be cultivated on bacteria (*Micrococcus* no. 6) where reproduction goes on copiously. In sterile soil, sterile soil suspension and sterile water the animals died within 6, 4 and 7 days respectively.

This in connection with the fact that bacteria are seen in the gut of most individuals from natural habitats allows the conclusion, that the species normally feeds on bacteria.

Choanolaimus psammophilus has not been studied under experimental conditions. According to direct observation it feeds on other nematodes. During 13 hours one individual had devoured 19 smaller marine nematodes kept in seawater in a watch glass.

Ethmolaimus pratensis has almost always bacteria in the gut when individuals from natural environments are examined. No culture experiments were performed.

Chromadora ratzeburgensis has often chlorophyll in the gut, and on two occasions I have found unicellular algae in the oesophagus. This in connection with direct observations of *Micoletzky* (1925) is in favour of this author's opinion that the species feed regularly on algae, perhaps especially diatoms.

Wilsonema auriculatum contains regularly bacteria in the oesophagus, and I have never seen other recognizable food substances. The same applies to *W. otophorum*, on which no culture experiments were carried out.

W. auriculatum can be reared on bacterial suspensions (of *Micrococcus* no. 6). Hatching, growth and reproduction seem to be normal.

Rhabdolaimus terrestris. In most individuals bacteria can be identified in the oesophagus. Nu culture experiments have been performed.

Plectus granulosus. Bacteria are generally found in the gut. Other substances are rarely seen.

This species can be reared on bacteria. Almost all the bacteria mentioned in table 20 could be used as food, however, all the species were not equally suitable. The most successful cultures were based on *Micrococcus* no. 6. The three other strains of *Micrococcus* were excellent food too.

Sarcina sp. could be used as food for adult individuals, however, the cultures did not develop as fast as those on *Micrococcus* no. 6, and the larval mortality was 80 %. Exactly the same applies to *Bacillus cereus mycoides.* Suspensions of no. 16 was a suitable substratum.

Stock cultures of the species can be reared on agar plate cultures of *Micrococcus* no. 6. The plates must be kept moist by watering every three or four days. This procedure proved better than the constant presence of a water film. In this latter case the hatching percentage decreased.

In sterile soil suspension and sterile soil the individuals died within 4—6 days.

Plectus cirratus generally contains bacteria in the gut, often 5—6 balls of bacteria are found in the oesophagus, and the anterior half of the digestive part of the gut may be completely blocked with bacteria.

The species may be cultivated easily on bacteria but not on sterile soil solutions. Experiments were only performed with suspensions of *Micrococcus* no. 6 and nr. 13.

Plectus rhizophilus, P. longicaudatus and *P. communis* generally contain bacteria, often in great numbers.

In a small dish with ca. 5 cc water containing bacteria 8 ♀♀ of *P. rhizophilus* lived for 22 days. Reproduction was copious, but the hatching percentage was extremely low, ca. 10, perhaps on account of oxygen deficiency — the water surface was covered by a heavy pellicle of bacteria. Other culture experiments have not been carried out in these species.

Plectus parvus always contains bacteria.

It is easily cultivated in suspensions of bacteria. All the species mentioned in table 20 except *Leptothrix ochracea* were offered as food, and all of them were suitable as food for adult individuals. Newly hatched larvae could not be reared, or at least only with great difficulty, in suspensions of *Sarcina* and *Bac. mycoides.*

Sterile soil suspensions and sterile soil could not be used as a medium, as all the individuals died within 7 days.

Theristus setosus. Culture experiments were not carried out with this species, but by way of direct observation it was found that the marine rotifer *Colurella amblytelus* (Gosse) was part of the normal food, as mastaces of this common species occurred in several individuals. *Schneider* (1906) reports diatoms *(Pleurosigma sp.)* as food and *Hofmänner* (1913) diatoms.

Monhystera vulgaris often contains bacteria, however not as often as do several of the preceding species. Like in *Prismatolaimus dolichurus* the gut often shows a dark coloration. Like *P. dolichurus* it is possible to rear this species on bacteria (*Micrococcus* no. 6), and the eggs will hatch normally, the larvae attain the adult state with a high reproductive rate, however, the dark coloration is not seen. Consequently it cannot be decided whether bacteria are the normal food of this species in nature.

Rhabditis monhystera. From the literature it has been shown (see p. 82) that the species of *Rhabditis* normally live on bacteria. Most investigations have been performed on *Rh. teres,* but according to my experience the same applies to *Rh. monhystera,* and according to *Teunissen* (1939) also to several other species.

All the organisms of table 21 with the exception of *Leptothrix ochracea* were tested as food. All of them were utilized by adult specimens except the yeast *Cryptococcus,* while the newly hatched did not thrive in suspensions of *Sarcina* and *Bac. mycoides.*

To get an idea of the probability of *Collier's* suggestion that the nematodes do not feed on the bacteria but on the partly decayed agar some experiments were carried out. An asparagin manitol agar plate culture was used for this purpose. *Rh. monhystera* thrived well on the plate which had been inoculated with an unknown bacteria isolated from soil. Subsequently the surface of the plate with bacteria was scraped off and transferred to a tube with sterile water. A sterile filtrate obtained by filtering through a porcellain filter stab was used as a substratum for sterilised eggs of *Rh. monhystera* in a moist chamber. 20 eggs were transferred, 18 hatched, but within 5 days all the larvae had died. In a parallel experiment with a suspension of the original culture serving as a medium 17 larvae hatched and 16 attained the adult stage within 7 days, one died during the second ecdysis (on the whole the ecdyses often will involve a certain mortality). Thus there is no doubt that the nematodes really feed on bacteria. The same is demonstrated by employing sterile soil and soil extract as a substratum. These experiments show that heat killed bacteria and dissolved and undissolved substances are not utilized as food, as the animals die within a few days. If ♀♀ with uterine eggs are transferred to sterile soil suspension, generally 2—3 eggs are deposited, subsequently the reproductive activity comes to a stop. The same is usually the case when other nematodes are transferred to an insufficient substratum, while in the case of sufficient substratum, the number of eggs laid per day remains almost constant. The fact may be illustrated by two examples. *Plectus parvus* and *Aphelenchoides parietinus*, 1 ♀ of each, were transferred to a suspension of *Micrococcus* no. 6. During the subsequent 9 days the number of eggs laid per day was in *Plectus parvus:* 6, 5, 6, 7, 4, 9, 5, 4, and 4. In *Aphelenchoides parietinus* the numbers were: 3, 2, 0, 1, 0, 0, 0, 0, and 0, the egg production ceases in this case, while the animal was still alive 20 days later.

Teratocephalus terrestris often contains bacteria. The species could be easily reared in suspensions of *Micrococcus* no. 6.

Acrobeles ciliatus usually contains bacteria. Like the preceding species it can be reared in suspensions of the same bacteria and in addition in *Actinomycetes* colonies in agar plates.

A. vexilliger has in most cases been found to have bacteria in the gut. No experiments were performed with this species.

All the species of *Cephalobus* examined by me *(C. nanus, persegnis, striatus, oxyuroides, elongatus* and *longicaudatus)* besides the related species *Macrolaimus crucis* and *Panagrolaimus rigidus* generally have bacteria, often in great quantities, in the gut.

In experiments it was very easy to rear *Cephalobus nanus, persegnis, oxyuroides* and *elongatus* on *Micrococcus* no. 6. The same applies to *Panagrolaimus rigi-*

dus and *Macrolaimus crucis*. Experiments have not been performed with the other species mentioned.

Bunonema reticulatum. Bacteria have been found regularly in the gut contents. Experiments have not been performed.*)

Tylenchorhynchus dubia. Recognizable gut contents are never seen. In experiments the species can be maintained in suspensions of *Micrococcus* no. 6 and no. 16, however, no eggs are produced.

Exactly the same applies to *Rotylenchus robustus*, *Tylenchus filiformis*, *Paraphelenchus pseudoparietinus* and *Aphelenchoides parietinus*, in addition the last species could not be maintained in suspensions of *Leptothrix ochracea* + other bacteria.

Thanks to the above experiments it has been possible to find suitable substrata for several freeliving soil nematodes. Where the experimental results are in agreement with direct observation of the gut contents of the respective species, it has been concluded that the substratum in question is utilized in nature too. To what extent this is the case cannot be decided, e. g. we are not able to tell if the liquid substances ingested together with bacteria are absorbed.

In case of bacteria the most clear results were obtained. There is no doubt that they constitute the chief food of the species in question, even if accessory food substances may be utilized. In no case was it found that particulate substances from the soil could be used as sole food, and there is no reason to believe this is the case in any nematode in nature as such substances have never been found in the gut in the necessary quantities. To me it is impossible to understand how this suggestion has been advocated at all, as simply nothing is in favour of it.

Several experiments have been recorded in literature stating the food of certain nematodes as "decaying meat", "plant matter", "egg white" etc. These experiments were generally carried out with unsterile media, thus they are inconclusive.

It is interesting to note, that all the species of nematodes which have been reared on these substances correspond exactly to those which I was able to cultivate in suspensions of bacteria, with the exclusion of other substances which are liable to involve errors of interpretation. Thus *Cephalobus subelongatus* was reared in water with parts of maize grains, leaves and stalks *(Steiner* and *Heinly* (1922)). Several species of *Rhabditis, Diplogaster, Cephalobus, Acrobeles, Plectus, Macrolaimus* and *Alaimus* were cultivated by *Maupas* (1901) on substances such as egg white, putrefying meat etc. and several other experiments have been carried out by others on species of the same genera and on similar substrata.

Thus with respect to the nematodes previously termed "saprozoitic" or the

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*) Later experiments have confirmed that this species can be reared successfully on bacteria *(Micrococcus sp.)*.

Table 22.

Species	Chief food as evidenced by direct observation (o) and experiments (x)				Source of information l=statements in the literature o=own investigations
	plant roots	bacteria	algae	other animals	
Alaimus primitivus		o x			o
Tylencholaimus mirabilis			(o ?)		o
Dorylaimus carteri and *obtusicaudatus*			(o ?)		l, o
Tripyla setifera				o x	l, o
Prismatolaimus dolichurus		(x ?)			o
Mononchus papillatus				o x	l
Ethmolaimus pratensis		o			o
Achromadora dubia		o x			o
Choanolaimus psammophilus				o	l, o
Punctodora ratzeburgensis			o		l
Wilsonema auriculatum		o x			o
Wilsonema otophorum		o			o
Rhabdolaimus terrestris		o x			o
Plectus granulosus, cirratus, rhizophilus, parvus		o x			o
Plectus longicaudatus, communis		o			o
Monhystera vulgaris		(x ?)			o
Theristus setosus			o	o	l, o
Rhabditis monhystera		o x			l, o
Teratocephalus terrestris		o x			o
Acrobeles ciliatus		o x			o
Acrobeles vexilliger		o			o
Cephalobus nanus, persegnis, oxyuroides, elongatus		o x			o
Cephalobus striatus, longicaudatus		o			o
Macrolaimus crucis		o x			o
Panagrolaimus rigidus		o x			o
*Bunonema reticulatum**)		o x			o
Tylenchorhynchus dubia	o				l
Rotylenchus robustus	o				l
Tylenchus filiformis	o				l
Aphelenchoides parietinus	o x		(o ?)		l
Paraphelenchus pseudoparietinus	o				l

*) see foot-note on p. 89.

like I have come to the same conclusions as does *Chapman* (1931) in the case of insects: "We shall next turn our attention to saprophagous insects. These are usually defined as those feeding upon decaying and fermenting matter. It is evident at the start, that these insects live in media which may be teeming with micro-

organisms. The evidence before us at the present time seems to indicate that in general they feed eventually upon microorganisms, and that the decaying material is the medium upon which the microorganisms live."

In practice it was impossible to test the nutrition of all species of freeliving nematodes. However, representatives of the most important genera were investigated by means of direct observation and experiment. From the results obtained certain generalisations were made within the different genera provided direct observations and morphological peculiarities did not contradict the conclusions. It may be mentioned that the nutrition of freeliving nematodes will be treated in greater detail in a later paper.

By applying this procedure table 22 was obtained. Here the cheif food of the most important nematodes is shown as far as it could be made out.

3. Nutrition and morphology.

When the statements of table 22 are compared with certain morphological features it turns out that a correlation is found between the feeding biology and the structure of the anterior part of the intestinal canal.

The presence of a stylet seems to indicate that the chief food is obtained by sucking *(Dorylaimus, Tylenchinae)*. In these species a bulbus oesophagi may be absent (*Dorylaimus*) or a bulb without valves may be present (*Tylenchinae*).

In the species without a stylet a distinct mouth cavity may be present or absent *(Alaimus)*. In the large species with a distinct mouth cavity "teeth" or "rasping plates" are often present in the mouth cavity (*Mononchus spp., Choanolaimus spp., Ironus spp., Trilobus spp.*), while in *Tripyla spp.* the teeth are found in the oesophagus. All these genera are generally reported as predators feeding on other animals (nematodes, rotifers etc.). In the small species with a distinct mouth cavity teeth may be present *(Ethmolaimus spp., Achromadora, Punctodora)*. All these species could be reared on bacteria, or (in *Punctodora*) evidence was at hand that algae (unicellular, e. g. diatoms) constitute the chief food.

Among the remaining species a certain grouping is possible. A large group *(Wilsonema, Plectus, Cephalobus, Acrobeles, Teratocephalus, Panagrolaimus, Macrolaimus, Bunonema, Rhabditis)* are devoid of teeth in the buccal cavity but part of the oesophagus is developed into a bulbus with three valves functioning as a masticatory apparatus with a similar mode of action as the mastax of rotifers (the movements of these valves are easily seen during feeding). In a single species *(Plectus cirratus)* the anterior half of the bulb has in addition a rasping plate consisting of transverse rows of fine teeth. In *Plectus granulosus* valves are absent as in *Rhabdolaimus terrestris*, however, the bulb is strongly cuticularized inside.

Table 23.

type of food	genera	morphological features
liquid	Pharethrolaimus, Diphtherophora, Tylolaimophorus, Xiphinema, Tylencholaimus, Trichodorus Actinolaimus, Nygolaimus, Dorylaimus	with stylet oesophagus without bulb
	Tylenchinae, Hoplolaiminae	with stylet oesophagus with bulb devoid of valves
particulate	Ethmolaimus, Achromadora	mouth cavity with teeth bulb without valves
	Wilsonema, Plectus, Cephalobus, Acrobeles, Teratocephalus, Panagrolaimus, Macrolaimus, Bunonema, Rhabditis	mouth cavity without teeth bulb with valves (Except *Plectus granulosus)*
	Plectus cirratus	mouth cavity without teeth bulb with valves and rasping plate
	Alaimus, Bastiania	no special mouth cavity oesophagus without bulb
chief food not exactly known	Monhystera, Prismatolaimus	mouth cavity without teeth oesophagus without bulb
relatively large organisms	Monochus, Choanolaimus	large species mouth cavity with teeth or teeth and rasping plates oesophagus without bulb
	Tripyla	large species mouth cavity without teeth oesophagus with tooth but no bulb

The last morphological group consists of *Alaimus, Monhystera* and *Theristus.* Here teeth and oesophageal bulb are absent.

If we distinguish three types of food in the freeliving soil nematodes a reasonable grouping of the total typical soil fauna (except a few very rare species which I have never seen) becomes possible (table 23). The three types of food are:

1. liquid food (especially plant juice), 2. particulate food (especially bacteria and small algae) and 3. relatively large organisms (protozoa, nematodes, rotifers etc.).

In the table all genera which could be conclusively referred to the group in question have been underlined with a continuous line, while in the genera where probability is in favour of the grouping adopted a hatched line is used, and the genera which have not been examined are without any line.

The table is proposed as a hypothesis, which can only be confirmed by way of further investigation. The sum of evidence in favour of this correlation of biological and morphological features which can be gained in true freeliving nematodes is nearly exhausted, but much valuable information can be compiled from a study of the feeding biology of the freeliving larval stages of parasitic nematodes. In several of these *(Strongyloidea)* "rhabditiform" larvae occur. They are charaterized by having a mouth cavity and oesophagus of exactly the same type as in freeliving rhabditids (cylindrical mouth cavity without teeth, oesophagus with isthmus and bulb with valves). According to the above hypothesis these larvae might be expected to feed upon particulate food (bacteria), and in fact *McCoy* (1929) has found this to be the case in *Ancylostoma caninum* (see p. 79). When changing to the infective stage mouth and oesophagus are modified together with the nutrition. The adult *Ancylostoma* sucks blood from the intestinal wall (*McCoy* (1935)).

Most of the ideas suggested in the preceding scheme have been touched upon by several authors as more or less vague concepts. The main deviations introduced here consist in stressing 1. that a large group of nematodes feeds on particulate food which is not "humus" or the like but bacteria, and 2. the possibility of correlating nutritional and morphological facts: All the species (except *Alaimus*) feeding on particulate food possess teeth in the mouth cavity or in the oesophagus or valves in the oesophageal bulb which are active in triturating the food. The oesophageal valves in these species act like the mastax of rotifers.

4. The reproductive rate.

The reproductive rate of freeliving soil nematodes is significant for certain considerations of the importance of these animals in soil biology. The facts which can be given here are not directly applicable to the soil as they were obtained from animals cultured in suspensions of a single species of bacteria. Probably the food supply is liable to modify the reproductive rate and the growth rate, and we do not know the supply of bacteria in soil, not even if we know the bacterial number, because the motility of the nematodes and the structure of the soil is important too. Secondly, the experiments were carried out at a temperature of

Table 24.

species	time required to develop from egg to egg in days	temperature ° C.	References
Alaimus primitivus	20—30	20 -22	
Tripyla setifera	30—40	20—22	
Prismatolaimus dolichurus	20—30	15—16	
Mononchus papillatus	ca. 50		*Steiner* and *Heinly* (1922)
Achromadora dubia	ca. 20	15—16	
Wilsonema auriculatum	ca. 20	15—16	
Plectus granulosus	ca. 25	15—16	
Plectus cirratus	20—25	20—22	
Plectus parvus	ca. 20	15—16	
Rhabditis teres	2—6		*Dotterweich* (1938)
Rhabditis monhystera	ca. 15	15—16	
Acrobeles ciliatus	20—25	15—16	
Cephalobus persegnis	ca. 20	15—16	
Cephalobus oxyuroides	ca. 20	15—16	
Cephalobus elongatus	ca. 15	15—16	
Panagrolaimus rigidus	ca. 15	15—16	
Anguillulina pratensis	ca. 45		*Gadd* and *Loos* (1941)

15—16° C or — in an older series of experiments — at 20—22° C, and certainly the temperature will influence the growth and reproductive rate significantly.

Under the circumstances of the experiments the following intervals were noticed between egg laying in two subsequent generations. In addition a few statements from the literature are given, (table 24).

The table may give an idea of the order of length of the time required for replacement of the animals in the soil. However, it must be kept in mind that variations occur, and that the circumstances of the experiments were not standard.

The number of eggs normally laid per female cannot be estimated at the present time. It is a very difficult question because we do not know how often copulation takes place in the different species or if parthenogenetic reproduction (eventually hermaphroditic) is normal. Thus the question must be postponed to a later treatment. That the reproductive rate may be high is seen from the fact that 1 ♀ of *Plectus parvus* produced 96 eggs within 16 days and in *Cephalobus elongatus* the rate even reached 209 eggs within 22 days. The numbers will become more impressive when it is stated that the eggs are very large in comparison with the animals. Thus in *Cephalobus* the measures were ca. 50 × 20 μ, while the weight of the mother was ca. 1 γ. This means that the egg production within 22 days exceeded 500 % of the weight of the mother. Compared with hens (specialized egg producers) it turns out that the percentage is higher than the values per year given by *Brody* (1945) for Plymouth Rocks, Wyandottes and Rhode Island Reds while it is of the same order as that given for White Leghorns.

10. ECOLOGICAL GROUPING AND IMPORTANCE OF FREELIVING NEMATODES

1. Ecological grouping and distribution.

In chapter 5 (see table 17) it was shown that most nematode species occur in all types of biotopes, the only exception being three species restricted to sand (*Tylencholaimus mirabilis*, *Acrobeles ciliatus* and *Tripyla setifera*), three to raw humus and moss (*Acrobeles vexilliger*, *Wilsonema otophorum* and *Bunonema reticulatum*) and a larger number of species which are only found in freshwater and permanently moist localities irrespective of the nature of the soil. The differences between the fauna of various localities are thus mainly quantitative which is apparent also from the fact that the dominants of all localities investigated comprise 21 species only (among ca. 100 possible) disregarding those which are framed in table 17 as being restricted to certain types of biotope (see table 18). Thus the general impression is that nematodes occur in all biotopes, the most diverse localities to a large extent exhibiting qualitative homogeneity but quantitative heterogeneity.

On the basis of the individual species the analysis of distribution could not be carried further in my material, which is fairly large.

In chapter 9 it was shown (see table 23) that the entire soil fauna of nematodes could be grouped satisfactorily according to food requirements and feeding biology:

1. Most *Dorylaiminae* feed on plant juices, to some extent at least from algae. The food is obtained by means of a stylet.

2. The *Tylenchinae* and *Hoplolaiminae* obtain their food in the same way but mostly from roots of higher plants (perhaps also from hyphae of fungi in some cases).

3. A large group feed on particulate food, mainly bacteria. It comprises certain *Chromadoridae* (*Ethmolaimus, Achromadora*), *Araeolaimidae* (*Wilsonema, Rhabdolaimus, Plectus*), *Anguillulidae* (*Rhabditis, Teratocephalus, Acrobeles, Cephalobus, Macrolaimus, Panagrolaimus, Bunonema*), *Dorylaiminae* (*Alaimus*).

4. Certain *Dorylaiminae* (*Tripyla, Mononchus*) and certain *Chromadoridae* (*Choanolaimus*) are predators feeding on protozoa, rotifers, nematodes etc.

5. In certain *Dorylaiminae* (*Prismatolaimus*) and *Monhysteridae* (*Monhystera*) the natural food is not known but bacteria will allow the species to reproduce under conditions of experiment.

Instead of considering the distribution of the single species we may analyse the distribution of the nutritional groups as ecological units. When this method is chosen some general ideas can be stated as to the importance of the five groups in different types of locality.

In table 25* all my localities mentioned in this paper have been arranged according to increasing density of nematode population in 1. mineral soils, 2. raw humus and 3. permanently moist localities. In each locality the following values were calculated:

1. the total number per sq.m. in thousands (based on tables 2 and 4—16),
2. the total weight per sq.m. in gs (based on tables 1, 2 and 4—16) and
3. the total respiration in cc 0_2 per sq.m. per hour at 16° C. (based on tables 1, 2, 4—16 and p. 68).

In the case of number, weight and respiration the percentage importance of each of the five groups was calculated.

If we consider the not permanently moist mineral soils it is seen that

1. grass fields harbour the densest nematode fauna, the numbers per sq.m. ranging from 4—20 million, while in all other localities the number does not exceed 2.5 million.

2. the same applies to weight, however, with some irregularities. Weight in grass fields 6—17.8 g per sq.m., outside grass fields 0.7—8 g.

3. the total respiration expresses the same fact. In grass fields an oxygen consumption was calculated amounting to 5.8—17.3 cc while the corresponding value in other localities is 0.6—4.6 cc.

If the fertility of all those localities could be directly compared and expressed in common units the nematode population might possibly be correlated with these indices. However, this being impossible, it seems justifiable to regard the degree of cover of the vegetation as an indicator of the size of the nematode population — and for practical purposes of the fertility too — and we may conclude that the size of the nematode population increases as the density of the vegetation increases in mineral soils (at the same time the root content of the upper layers of the soil will generally increase too).

The average percentage importance (based on respiration) of the groups feeding on 1. bacteria, 2. roots and 3. algae in relation to the density of the total fauna is seen from table 26:

1. the relative importance of bacteria feeders increases from 7—47 % as the total population increases from 175 000—20 000 000 nematodes per sq.m.,

2. the relative importance of root suckers increases from 4—16 % within the same range of the total population, while

3. the relative importance of alga feeders decreases from 88—28 %.

A complete evaluation of these facts cannot be made until counts of bacteria and algae from the localities in question are at hand. However, the general trend seems to agree with the concept that mineral soils of low microbiological activity and low fertility harbour a poor nematode fauna among which the alga feeders

Table 26.

% importance (based on respiration) of species feeding on	bacteria	roots	algae
mineral soils			
total population per sq.m.			
175 000—800 000	7	4	88
1—8 million	27	9	51
10—20 million	47	16	28
raw humus			
1.2—2.7 million	27	10	52
constantly moist soil			
330 000—1 500 000	18	7	65

are the most important, while mineral soils with high microbiological activity, high degree of plant cover and high fertility seem to harbour a rich nematode fauna where bacteria feeders and root suckers are important groups too.

That the supply of food is an important factor in the distribution of these nutrional groups seems reasonable, but in addition the dense plant cover may act physically in stabilizing the moisture relations (conservation of water by depressing evaporation). This does not oppose to *Stålfelt's* (1937) view, that a vegetation of herbaceous plants will increase the evaporation from the soil. This is surely the case when the total evaporation is considered, but it must be remembered that a very large proportion of the fauna is concentrated in the upper few milimeters of the soil and in the often very inconspicuous detritus layer upon the soil, i. e. in layers from where plants will generally not draw their water). Which of these two effects is the most important one cannot discussed in general terms. However, the plant cover must be considered, directly or indirectly. In the rye field and still more distinctly in the turnip field at Studsgaard (table 9) plots are present of even very high fertility in comparison with natural localities, nevertheless the nematode fauna is poor, only amounting to about 1 million individuals per sq.m.

The most reasonable way in which to describe the distribution of nematodes is probably obtained when it is remembered that the non-marine nematodes must be characterized as freshwater organisms which have later on invaded the soil and moss cushions. Almost all authors agree in this concept (see e. g. *Steiner* (1922), *Stauffer* (1925) and *Gislén* (1947)).

Micoletzky (1925) gives a tabular survey of the number of the different species of nematodes found by him in freshwater and—as far as can be ascertained—permanently moist soil in Denmark. The material comprises 9007 specimens. If the soil localities are disregarded and the numbers are recalculated to weights on

Table 27.

% importance (based on weight) of species feeding on	bacteria	roots	algae	animals	unknown food
freshwater	2	0.05	**48**	**49**	1
permanently moist soil	14	6	**71**	8	2
normal soil	**33**	12	**43**	5	4
extremely dry soil	7	2	**88**	1	1
raw humus	21	11	**57**	8	3
moss	**62**	8	13	15	2

the basis of *Micoletzky's* measurements and my method described p. 15, we obtain some values of relative weight distribution of the different nutritional groups. Of course, the values are not as exact as in the case of my own soil material, however, they give a good idea of the order of magnitude. Absolute values cannot be given, because the paper by *Micoletzky* is not based on quantitative concepts. As to the species of *Chromadora,* which do not normally occur in soil, they have been assumed to be alga feeders, a point of view which seems justifiable on account of numerous observations of algae in the gut content. The same applies to all species of *Dorylaimus,* even if the exact food is not known. Corresponding values from all the soil localities are drawn from my table 25 by calculating the average weight percentage of the groups in question in each of the soil types: permanently moist soil (localities 27—31), normal soil (i. e. soils where the moisture conditions are nearly optimum so as to allow agricultural utilization) (localities 6, 11—22), extremely dry soil (localities 1—5, 7—10), and raw humus (localities 23—26), while the weights in moss were calculated from table 2 in my previous paper (*Overgaard* (1948 b)).

In this way table 27 is obtained. During the natural sequence: freshwater-permanently moist soil — normal soil — extremely dry soil certain essential differences are found.

Freshwater harbours a large mass of predators (especially *Trilobus, Tripyla, Mononchus* and *Ironus)* and alga feeders (especially *Dorylaimus* and *Chromadora*) while the root suckers (*Tylenchinae*) are almost absent and bacteria feeders are of small importance only.

In permanently moist soil the alga feeders dominate (especially *Dorylaimus*).

In normal soil the same applies but in addition bacteria feeders are important (especially species of *Plectus, Cephalobus, Acrobeles* and *Teratocephalus*).

In extremely dry soil the alga feeders are of decisive relative importance (especially *Dorylaimus* and (in sand) *Tylencholaimus*). This seems rather contradictory, but it must be remembered 1. that the number of algae may be

very high in such localities (see e. g. *Petersen* (1935)) and 2. that it has not been demonstrated conclusively that algae are the chief food of these species.

In raw humus the alga feeders (especially *Dorylaimus*) are fairly important while the significance of bacteria feeders has decreased. This is in close correspondance with the fact that bacteria are less numerous in this soil type (see e. g. *Romell* (1935)). It may be mentioned here that oribatids — which to a large extent feed on fungi — are extremely common in raw humus while their abundance in mineral soils is much less (see e. g. *Forsslund* (1943) and *Weis-Fogh* (1948)).

In moss the nematode fauna has quite another character (see *Overgaard* (1948 b)) as bacteria feeders are the most important group (especially *Plectus rhizophilus* and other species of *Plectus*), while predators (especially *Mononchus papillatus*) may be fairly important in certain localities. Alga feeders are generally not important, even if *Dorylaimus carteri* may be common in some places. The importance of root suckers is generally small, the most common species being *Tylenchus davainei*, which often attacks the chlorophyll bearing parts of mosses thus producing galls.

This is in good agreement with the fact that moss cushions are well aerated and display a large surface with good conditions of growth for bacteria when water is present. However, the cushions are often desiccated during shorter or longer periods, thus the nematodes living here must possess the power of surviving these intermittent periods of drought which in fact they do. In addition the typical moss fauna has certain locomotory possibilities which enables it to exploit the large leaf and stem surfaces (*Overgaard* 1948 b)). The fauna of permanently moist moss cushions corresponds to that of permanently moist soil (1. c. table 4).

The importance of the species of *Dorylaimus* and *Mononchus* in the different sample series can to some extent be deduced from the average weight of the nematodes (in γ). In the different localities this value is given in the last column of table 25. A high average weight indicates a large percentage of species of these two genera as most of them are essentially larger than the remaining species.

2. Importance of nematodes.

a. Importance of nematodes in comparison with other soil organisms.

Several authors have tried to estimate the weight of all organisms of the soil per ha or other areas. In doing this resort has been taken to approximations and generalizations by introducing concepts of "average populations". In spite of the numerous errors involved such considerations may be very informative.

As an example I refer to *Stöckli's* table 1 (1946 a). The contents of this table

may be summarized for my purpose by stating the following weights per ha (depth 0—15 cm):

microflora	20 219 kg
protozoa	379 -
nematodes	50 -
enchytraeids	15 -
earthworms	4 000 -
mites, collembola, protura, diplura	11 -
other invertebrates	797 -
total	25 471 kg

There is no reason to discuss details of the table, some groups may be underestimated, others overestimated. In principle the table gives a good idea of the distribution of living organic matter in a natural grass field.

Certain facts may be pointed out:

1. the most important group of organisms as to weight is the microflora (bacteria, actinomycetes, algae and fungi) constituting ca. 80 % of the total weight of the organisms,

2. the groups which generally occur as a microfauna (protozoa, nematodes, mites, collembola, protura and diplura) constitute a very small fraction, only ca. 2 %, while

3. the remaining invertebrate fauna constitutes ca. 18 %.

4. Within the microfauna protozoa are the most important animals constituting ca. 86 % of the weight, while nematodes constitute ca. 10 % and microarthropods the remaining 4 %.

Thus we may sum up: next to protozoa nematodes are the most important component of the microfauna, which in turn constitutes ca. 2 % of the total weight of organisms in a grass field like that investigated by *Stöckli.*

A total weight of 25 471 kg per ha seems large. A better impression of the organisms in relation to the inanimate environment is obtained when calculated to dry weight. Assuming a water content of the organisms of 75 %, a volume weight of the soil of 1100 g/l and an average content of organic matter of 7 % as given by *Stöckli* (1946 b) for a similar locality we get: 1650 000 kg of dry soil per ha of which 115 000 kg is organic matter. Assuming that 10 % of the organic matter is constituted by roots, a percentage which seems reasonable when compared with *Weis-Fogh's* (1948) results, the relative importance of the different fractions is (expressed in kg dry weight per ha):

115 500 kg organic matter consisting of
11 550 kg plant roots
6 368 kg other organisms and
97 582 kg dead organic matter.

As mentioned above, this survey does not claim to be exact, however, it may illustrate the fact that competition may be severe, an experience with which most practical farmers are familiar, and which is fairly easy to imagine when it is remembered how large a proportion of the total organic matter may be present as living organisms all of which are active in this competition.

The large number or weight of living organisms in the soil involves that the farmer cannot add a certain amount of plant nutrients in such a way that all of it is utilized directly by the plants. It is added to the soil where the different organisms, among these higher plants, will compete for it.

It may be appropriate to trace the three fractions of organic matter a little further.

When plants or parts of plants die they return to the soil where they are decomposed to simpler organic combinations and in due time to inorganic substances identical with those originally utilized by the living plant.

Several organisms are active in this mineralization of organic matter, simultaneously as well as successively. If the soil be fertile this interaction of different organisms is necessary because a single species is not able to bring about the complete mineralization. Several organic substances of plants and animals are easily decomposed (e. g. proteins) while others are very resistant to decomposition (e. g. lignin, especially fungi being responsible for the decomposition of this substance). The final products of the easily decomposed substances consists of CO_2 and a very large number of inorganic and simple organic products which are utilized again. The organic matter resistant to decomposition accumulates as a dark, colloid substance generally termed "humus" of which the "humus nucleus" deserves special attention. It consists mostly of a complex of lignin and proteins which is very resistant to microbial decay, as the proteins seem to be "protected" in some way by lignin. (For the detailed concept of humus, see *Waksman* (1938)). A practical test of this progressive decay of original plant matter is furnished by the nitrogen: carbon ratio. In the fresh plant material this ratio is about 1 : 20—1 : 30 or less, during the decay the ratio increases to that of many soils, 1 : 9—1 : 12 (see *Anderson* and *Byers* (1934)), thus tending towards that of the microorganisms themselves (in fungi 1 : 10, in bacteria 1 : 5 (*Waksman* and *Starkey* (1931)), where it remains. During the course of this decomposition process all the soil organisms are active, each group with its maximum activity at different periods attacking different substances and liberating different end products. The continuation of the

process is made possible by the constant addition of fresh plant material and dead bodies of the organisms bringing about the decay.

Now, it is evident that the fertility of a soil does not depend upon the quantities of organic matter present but upon the tempo of the mineralization. It is in this state the chemical constituents are utilized by plants. The soil organisms contribute in widely different ways to this process. Some of them attack the original organic matter, one fraction of it being converted to living protoplasm, another partly serving as a source of energy (generally the carbon containing substances, which are transformed to $C0_2$, hence the increase in the N : C ratio during the decomposition) while a third fraction is liberated as waste products, that may be attacked by other organisms; especially ammonia and urea are easily available.

The most important organisms bringing about this primary cycle are bacteria, fungi, actinomycetes and algae, while several animals probably contribute essentially to it (e. g. oligochaeta). In addition to the primary cycle the mere presence of the enormous numbers of bacteria etc. creates the possibility of several cycles of higher order, the members of which feed upon those pertaining to the primary cycle. The presence of these accessory cycles probably contributes to the rapid circulation of the nutrients. If the vegetation consisted exclusively of trees and the litter was removed, the soil would soon run short of available nutrients because several years would pass before the inorganic substances taken from the soil would be returned to it as organic matter to be mineralized again. In addition the mineralized products are to some extent lost by drainage, especially the nitrates, which do not enter into the ion exchange complex of the soil in contrast with most other ions. The presence of the soil organisms has among others the effect that organic matter is returned more often (because they generally live for a much shorter time than the plants) so one single atom of say nitrogen may possibly pass the inorganic state (ammonia or nitrate) several times a year as most animal substances are easily decomposed (see *Lindquist* (1941)). Thus the soil organisms have at least two important functions: 1. to bring about a mineralization of plant residues and 2. to act as a certain reserve (or buffer) of easily available and rapidly circulating substance. Perhaps this stimulating effect of the soil fauna is the most important of all its functions and much more beneficial than the direct contribution to the degradation of the organic matter (which is probably carried out much more effectively by the microflora).*)

A prime task of soil biology is to demonstrate to which of

*) In addition the mechanical action of the macrofauna must be mentioned. In virgin soils it is important while in cultivated soils part of this action has undoubtedly been taken over by ploughing and other refined soil treatments.

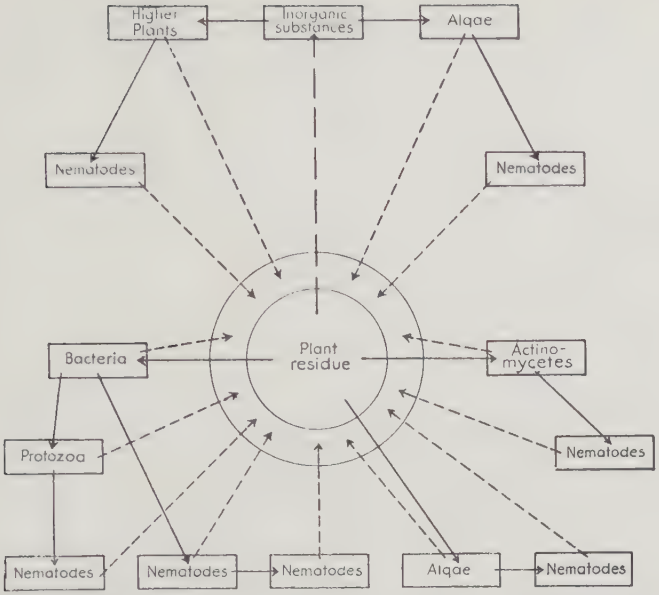

Fig. 16. Diagram of the chief links of the food cycle of freeliving nematodes. The dead organic matter of the soil is thought to consist of original plant residue (centrally) and dead bodies deposited during the cycle represented. ———— = enter into, ····· = turn into when dead, — — — — = enter into through several steps involving mineralization.

those possible cycles the individual animal groups belong, or for which cycle the activity of the group in question is most important.

As to nematodes there is no doubt that they belong to cycles of secondary or higher orders. None of them feed upon inanimate organic matter, on the contrary they obtain their organic matter from other organisms pertaining to the primary cycle (those feeding upon bacteria and (heterotrophic) algae, see table 23), to the secondary (those feeding on other nematodes) or cycles of much higher order, after mineralization (those feeding on roots of higher plants and on (autotrophic) algae). On account of their rapid succession of generations (see table 24) the organic matter is returned to the stock several times a year. The position of nematodes in the processes of decomposition is illustrated diagrammatically in fig. 16.

It is far from possible to arrange the total soil flora and fauna according to cycles, however, tentatively some cycles are suggested as follows, stressing that several statements have never been verified:

I. cycle: bacteria, fungi, actinomycetes, heterotrophic algae etc.
enchytraeids, earthworms, millipeds, certain insect larvae, isopods etc.

II. cycle: feeding on bacteria: certain nematodes, certain protozoa.
feeding on fungi: certain mites.
feeding on actinomycetes: certain nematodes.
feeding on heterotrophic algae: certain nematodes and collembola.
feeding on enchytraeids and earthworms: certain insects and vertebrates (in case of birds the organic matter is temporarily lost).

III. cycle: feeding on nematodes: certain nematodes, certain mites.
feeding on protozoa: certain nematodes.
feeding on mites: certain mites.
feeding on insects: certain insects and vertebrates.

?. cycle: feeding on plant roots: certain nematodes, insects, fungi, bacteria etc.

This superposition of different cycles makes a quantitative estimation of the importance of the different soil organisms extremely difficult because all the cycles must be considered simultaneously as they interact.

The discussion of nematodes in this connection must be restricted to those feeding on bacteria, because this is the only group in which we may compare with parallel investigations on other soil organisms with similar food requirements, namely protozoa.

As is known bacteria are able to bring about a very profound decomposition of dead organic matter. On the other hand the suggestion has been made that young cultures of bacteria contain more enzyme per weight unit, thus being more active than older cultures.

Beforehand the bacteriophagous nematodes may be thought to influence the bacterial population of the soil in either of two ways:

1. the food requirements of bacteriophagous nematodes will cause the n u m b e r of bacteria to decrease, simultaneously a reduction of bacterial a c t i v i t y may seem logical.

2. the reduction of the number of bacteria may cause an acceleration of the division rate, i. e. a rejuvenation of the bacterial population, which may involve an increase of biochemical activity.

We may assume an average population of nematodes amounting to 10 million per sq. m. and a weight of 12 g of which 1/3 feed on bacteria, thus we get 4 g per sq. m., corresponding to 4 0 k g p e r h a.

In comparison with protozoa this amount is rather small. According to *Stöckli*'s estimations (based on *Russell*) we have 3 7 9 k g o f p r o t o z o a, i.e. ca. 10 times the amount of nematodes, while the amount of potential food consists of ca. 1 0 0 0 0 k g o f b a c t e r i a. The amounts of protozoa and bacteria are in good agreement with those calculated on the basis of *Koffman*'s (1934) results (300 kg of active protozoa and 7000 kg of bacteria).

Until reliable respiratory rates of soil protozoa are available we may assume that the importance of these two groups is proportionate to their weights, thus 90 % of the eventual reduction of the number of bacteria is due to protozoa and 10 % to the bacteriophagous nematodes.

The importance of protozoa has been discussed in several papers since *Russell* and *Hutchinson* (1909, 1913) suggested their "protozoan theory of soil fertility" mainly on the basis of experiments with "partial sterilization" of the soil, i. e. the treatment with heat or desinfectants, especially toluene. The theory may be briefly summarized: The soil protozoa feed on bacteria thus limiting the number and activity of these. By means of partial sterilization the protozoa are destroyed while the bacteria are only suppressed. After this initial suppression the bacteria develop without being hampered by the protozoa and with a consequent increase of the nitrate production.

The results of the several reinvestigations of the importance of protozoa are highly contradictory, *Russell* and *Hutchinson* (1. c.) considering protozoa very important, *Koffman* (1934) considering the influence small, while *Waksman* and *Starkey* (1931) take up an intermediate point of view.

The daily counts of bacteria and protozoa at Rothamsted throughout a year (*Cutler, Crump* and *Sandon* (1923)) confirm that a low number of protozoa is correlated with a high number of bacteria and vice versa, and several experiments involving a partial sterilization confirm the initial depression subsequent to this process. However in a few days the bacterial number rises to a maximum far exceeding the original number (in *Waksman* and *Starkey's* experiments (1931) by 500 %). As to the production of nitrate and ammonia the results are not so clear. In *Waksman* and *Starkey*'s experiments the production of these substances was increased by ca. 20 %, while *Koffman* (1. c.) did not obtain statistically significant improvements in the production of soluble nitrogen.

The different results obtained may indicate that the experiments cannot be compared directly as several factors are altered simultaneously. The mere application of heat or desinfectants may alter the soil considerably and alter the availability of the nutrients already present. The fact that treatment with heat and desinfectants of the same soil may give different results is in favour of this concept. In addition the following may be cited from *Koffman* (1934): "Überblicken wir den Stoffumsatz in den verschiedenen Serien, so finden wir, dass die Ammonifikation und Nitrifikation in guter Übereinstimmung miteinander stehen, und dass die Behandlung des Lehmbodens an und für sich einen viel stärkeren Einfluss auf den Stoffumsatz im Boden ausübte als die zugesetzten Protozoen."

Another factor which, as far as can be judged, has not previously been taken into appropriate consideration is the not unimportant quantity of easily

accessible organic matter which is mobilized by killing the protozoa and other animals besides a large proportion of the microflora.

Last but far from least *Russell* and *Hutchinson* and other authors have stressed the importance of bacteria in soil fertility. It must be admitted that they are important, but other organisms, e. g. fungi and actinomycetes are able to bring about a large number of the processes which have been regarded as bacterial. In *Waksman* and *Starkey*'s experiments an increase of the bacterial number by 500 % was recorded, however, at about the same time the number of fungi had increased by 300 %.

Thus no definite conclusions can be drawn as to the importance of protozoa in relation to the total microbiological activity of the soil. It seems probable, that they are able to reduce the number of bacteria considerably. Whether this reduction of numbers involves a reduction af bacterial activity too cannot be decided, even if it has been claimed to do so by several authors. On the other hand the presence of protozoa seems to improve the nitrogen fixation by *Azotobacter* (*Cutler* and *Bal* (1926), *Nasir* (1923), *Meiklejohn* (1930, 1932)). This may support the theory of increased activity of rejuvenated populations. However, as appears from *Gale* (1947) it cannot be universally accepted as several enzymes are not more concentrated in young than in older cultures.

After this discussion of the interrelationship between protozoa and bacteria it is obvious that the present state of our knowledge does not allow us to draw any definite conclusion as to the influence of bacteriophagous nematodes upon the bacterial activity. *Cutler, Crump* and *Sandon* (1922) have shown convincingly that there is a certain correlation of bacterial and protozoan number. This must be interpreted in such a way that the number of bacteria present is partly controlled by protozoa. On logical grounds nematodes must contribute in parallel with protozoa to the maintenance of this balance. The relative importance of protozoa and bacteriophagous nematodes cannot be stated until it is known how many bacteria are consumed by either of the groups. Until this question has been investigated it seems reasonable to believe that the influence of nematodes is of the order of size of 10 % of that of protozoa in ordinary mineral soils.

As to bacterial activity indications are at hand that a reduction of number involves a parallel reduction of activity. However, the opposite conclusion has been reached by several authors. The problem is a very complicated one as it must, at last, be a question of enzyme activity in relation to the age of bacterial cells and growth phase of bacterial populations.

With regard to the influence of a reduction of bacterial number upon the total microbiological activity the conclusions obtained are cont-

radictory and most experiments seem to be inconclusive as several factors are altered simultaneously during the partial sterilization. However, the fact must be stressed that a detrimental influence of soil protozoa upon the total microbiological activity of an intact soil has never been demonstrated. The treatments involved in a partial sterilization must to some extent act as a mobilisation of the nutrients contained in the now dead organisms. An identical point of view is held by *Romell* (1934) in connection with raw humus. The mere sampling and storage of the samples will cause a mobilization of nutrients hitherto bound up in living matter, especially fungi.

On this basis the action of a partial sterilization will result in a certain amount (not unconsiderable) of living protoplasm being killed off and the contained nutrients mobilized. On account of the often strong competition part of them will be absorbed by higher plants while others will allow the microflora to profit by them.

The depression of bacteria by protozoa and nematodes may involve a similar mobilization and perhaps allow other components of the microflora to flourish on the nutrients previously contained in the bacteria and to occupy the space previously held by bacteria. In this intermittent local activity the net microbiological activity need not necessarily be different. It may produce the same end result only proceeding along different paths.

However, the whole question cannot be solved except through the collaboration of microbiologists and zoologists.

The weight of nematodes present in comparison with other animals has been mentioned p. 100 ff on the basis of *Stöckli*'s table. Nevertheless, it might be interesting to consider some actual localities. Only a single locality allows such a comparison to be made, namely locality no. 8 af *Bornebusch* (1930) which is nearly identical with my spruce raw humus locality (table 14), either of them being located in the same section of Grib Forest (Sealand). However, the comparison cannot be exact as *Trägårdh* and *Forsslund* (1932) maintain that *Bornebusch*'s technique was not satisfactory with the result that he only obtained ca. 10 % of the mites and 2 % of the collembola present. I am not able to decide if these percentages are correct, however, on comparing with the numbers obtained by these authors in similar localities it seems likely. The following survey of the quantitative relations in this locality is an extract of *Bornebusch*'s table XII with the corrections suggested by *Trägårdh* and *Forsslund* on the assumption that *Bornebusch*'s technique of extraction was not selective and that his average weights of a single mite and collembola can be maintained:

	mg per sq. m.
Oligochaeta	1596
Myriopoda	1755
Araneina	67
Acarina	4490
Collembola	6850
Diptera	1034
Coleoptera	3797
other insects	987

to which may be added

Nematoda	4500

On account of the sources of error mentioned above the weight distribution cannot be discussed in detail. Nevertheless, it is evident that the microfauna (even without protozoa) is much more important in relation to the macrofauna than in the locality mentioned on p. 100. Thus we find 11 340 mg of mites and collembola + 4500 mg of nematodes = 15 840 mg of microanimals and only 9236 mg of macroanimals. The weight of nematodes is less than half the weight of microarthropods. (In comparison with other raw humus localities the weight of nematodes is even high here on account of the abundancy of *Dorylaimus abtusicaudatus)*.

When the regular and comprehensive sampling carried out in the grounds of the Mols Laboratory has been published a valuable material will be available allowing similar comparisons to be made within a wide range of biotopes, mineral as well as organic soils. At the moment the weight of nematodes can only be compared tentatively with *Weis-Fogh*'s investigations on mites and collembola.

In a raw humus locality (Rogeshøj) he found an amount of mites and collembola which I (on the basis of *Bornebusch*'s weights and the measures given in various papers) have calculated at 4—5 g per sq. m. while the weight of nematodes according to my sampling amounts to ca. 2 g per sq. m. in this locality. This is nearly the same relation as found in the previous locality.

In a mineral soil (Pl. I) the weight of mites and collembola has been calculated at ca. 2 g, while that of nematodes is 14 g.

The weight comparisons cannot be regarded as exact. However, they allow us to draw the conclusion that microarthropods (mites and collembola) constitute a larger weight than nematodes in raw humus and probably most organic soils, while in mineral soils the opposite distribution is found. Thus the importance of nematodes is most conveniently studied in mineral soils while that of mites and collembola will be most distinct in raw humus.

This is in agreement with the general impression obtained during practical field work.

The importance of mites and collembola in raw humus will not be discussed in this paper, but it is an interesting fact that *Forsslund* (1943) reaches almost the same conclusion as to the interrelationship between certain of these animals and soil fungi as that which I have reached with regard to bacteriophagous nematodes and bacteria.

b. The importance of nematodes in relation to the nitrogen cycle.

On the basis of the oxygen consumption it is possible to draw certain conclusions as to the importance of soil nematodes on the whole. In order to obtain a basis for discussion the calculations underlying table 25* are given in details for eight selected, typical localities (tables 28—35*). In addition to these values I have calculated the oxygen consumption of nematodes per ha at 16° C per vegetation period. This last term has been introduced as a compromise, "per year" being a more satisfactory standard. I have tried to calculate the annual mean temperature for some of the localities in Mols, however, it was impossible to get reliable values for some important months. Instead of assuming some arbitrary annual mean temperature I have chosen the procedure of considering a vegetation period of 100 days (medio May—ultimo August) and for this period a mean temperature of 16° C of the upper 5 cm of the soil has been adopted. To be judged from the measurements available this temperature is probably too low (within this period the morning temperatures of the upper cms. of the Plain were all of them above 16° according to *Weis-Fogh*'s (1948) measurements). When in some years, continuous temperature records are available at the Mols Laboratory the annual 0_2-consumptions will be published. Probably an approximation to the annual consumption is obtained by multiplying my figures by 2—3.

In chapter 9 it was shown that the food of nematodes consists of bacteria, algae, plant juices (mostly obtained from the roots of higher plants by piercing the cell walls of the roots) and nematodes and other organisms.

According to *Waksman* and *Starkey* (1931) bacterial dry matter contains 10 % N. If this is recalculated to crude protein according to current practice on the assumption that protein contains 16 % nitrogen (see e. g. *Comber, Jones* and *Willcox* (1947)) it is found that bacterial dry matter contains 60 % protein, the remaining 40 % is arbitrarily distributed between fat and carbohydrate, 20 % each.

As to the food of the other nematodes we may without any great error assume the same basic composition, as the walls of cells are not ingested. In plasmodia

of *Fuligo varians* the crude protein (protein, nucleoproteins, nucleic acid, amino acids, purine bases, asparagine etc.) constitute 60.3 % according to *Lepeschkin* (1926) and 56.5 % according to *Reinke* and *Rodewald* (1881). *Kiesel*'s (1930) analyses show the crude protein to constitute 44.75 % in plasmodia of *Reticularia lycoperdon* and 73.04 % in *Lycogala epidendron*. In the cytoplasm af cabbage leaves *Chibnall* and *Channon* (1927) found 63.1 % crude protein.

By assuming the general composition of the food of nematodes to be 50 % protein, 25 % fat and 25 % carbohydrates, the protein fraction has certainly not been overestimated.

For the estimation of the importance of nematodes in the nitrogen cycle of the soil it is assumed — as usual in this type of calculations:

1. that the combustion of fat and carbohydrate is complete,
2. that the three food fractions are utilized in the ratios in which they are present, i. e. protein: fat: carbohydrate = 2 : 1 : 1.
3. that the physiological combustion of

   1 g protein affords 1 liter 0_2,

   1 g fat affords 2 liter 0_2,

   1 g carbohydrate affords 0.83 liter 0_2.

On these assumptions the oxygen absorbed is distributed between the combustion of proteins, fats and carbohydrates as 0.50 × 1, 0.25 × 2 and 0.25 × 0.83 = 0.5, 0.5 and 0.208 = 1, 1 and 0.42.

Thus the absorption of 2.42 10_2 corresponds to the combustion of 1 g protein.

Applying this relation to the localities of tables 28—35 we obtain the following amounts of nitrogen combusted in kg per ha per vegetation period at 16° C (table 36). (1 kg. N is equivalent to ca. 40 kg fresh weight consumed when based on bacteria):

The nitrogen combusted has been converted to 1. nematode protoplasm, 2. excretory products (urea, ammonia or other substances, the definite composition is not known as yet (*Heidermanns* (1937)) and 3. casts (apparently the quantity of casts is very small. In my cultures I have never noticed any traces).

Thus the main part of the nitrogen must be assumed to be converted to easily available products which are liberated during the activity of the nematodes or subsequent to their death.

In order to get a better impression of the amounts given in table 36 it may be practical to compare with the amounts of nitrogen absorbed by higher plants. This is possible in the rye field at Studsgaard on the basis of *Hansen* (1948) and the crop analyses from the same plots during the years 1929—32 (*Kristensen* (1939)) and the nematode weights found by me. This comparison is given in table 37 from which it is seen that the amount of nitrogen mobilized by nematodes per

Table 36.

	O_2-consumption per ha per vegetation period at 16° C, in m^3.	kg N combusted per ha per vegetation period
Corynephorus slope, bare	15	1
High moor, Herning	30	2
Calluna heath, raw humus, Studsgaard	50	3
Meadow, mull	55	4
Rye field, Studsgaard	60	4
Calluna heath, sand, Studsgaard	110	7
The Plain I+II	300	20
Grass field, Studsgaard	415	27

Table 37.

treatment	yield, dry matter kg per ha		yield, kg N per ha		yield kg N total	N combusted by nematodes kg per ha per veget. period
	grain (86.5 % dry matter)	straw (86 % dry matter)	grain (in brackets % N in dry matter)	straw (in brackets % N in dry matter)		
unfertilized	865	1170	13.1 (1.51)	5.5 (0.47)	18.6	3
1/2 manure	1030	1645	15.1 (1.46)	7.7 (0.47)	22.8	4
1 manure	1300	2100	18.3 (1.41)	9.9 (0.47)	28.2	4
1 1/2 manure	1480	2560	20.4 (1.41)	12.0 (0.47)	32.4	5
1/2 fertilizer	1170	1840	16.1 (1.38)	8.1 (0.44)	24.2	4
1 fertilizer	1550	2690	20.5 (1.32)	11.0 (0.41)	31.5	5
1 1/2 fertilizer	1890	3430	25.6 (1.35)	14.1 (0.41)	39.7	4

vegetation period is of the order of size of 10 % of that removed by the crop when compensation has been made for the amount left in stubbles and roots. In the grass field the percentage seems to be still larger as the amount of nitrogen removed in the best plot of the fertilizer experiment (1 1/2 manure) corresponds to ca 110 kg per ha while 27 kg is combusted by nematodes per vegetation period.

When it is remenbered that nematodes constitute only a very small fraction of the total soil fauna (probably of the order of size of 1 % in most mineral soils) and that the annual values are probably ca. twice as high the figures seem to be large.

This means that the point of view presented p. 102 f. gains highly in probability: During the activity of the soil fauna fairly large amounts of nutrients are mobilized, loss of nutrients is to some extent counteracted and the tempo of the minerali-

zation is increased. This mobilization evokes a constant renewal of the competition for basic nutrients of higher plants and members of the microflora.

On the basis of our present knowledge it is not possible to give any figures of the net result of the activity of the total soil fauna, however, the results obtained from freeliving nematodes indicate that the effect cannot be neglected beforehand, even when the mechanical influences of the macrofauna are left out of consideration.

The question is very complicated as it involves an interaction of several widely different groups of animals obtaining their food from widely different sources. When soil fertility is the point from where these processes are considered some factors must be considered positive while others (e. g. the plant parasitic nematodes) are certainly acting in a negative direction, as they obtain their food directly from the very product of the agricultural fertility.

11. SURVEY OF TAXONOMY

This chapter serves the folowing purposes:

1. to give the reader not familiar with nematode taxonomy a survey of the classification and interrelationship of freeliving and parasitic nematodes. The classification adopted here is the one proposed by *Filipjev* (1934). The adoption of this classification does not mean that it must be considered the most probable one. Being unable to treat critically the taxonomy of parasitic nematodes, I have laid the main stress upon the fact that *Filipjev* has studied all groups of nematodes and that his papers on freeliving species are excellent. In addition the paper mentioned is easily accessible here,

2. to point out which nematodes are parasitic (indicated by (p)), marine (m) and freshwater and/or soil inhabitants (f), (s) and (fs) respectively,

3. to state the authors of all the species mentioned in this paper in order to remove a source of error which might be serious in several cases, and

4. to give a survey of the species known from Danish freshwater and soils by including those mentioned by *Ditlevsen* (1911) and (1921) and *Micoletzky* (1925). These species have been marked (D), (D 21) and (M) respectively. All species found by me are included in the list even if they have not been mentioned in the preceding chapters or in my previous paper (1948).

Classification of nematodes.

Order *ENOPLATA*
- Family Enoplidae (m)
- Trilobidae (m f s)
- Dorylaimidae (m f s)
- Mermitidae (p)

Order *ANGUILLULATA*
- Family Anguillulidae (p m f s)
- Tylenchidae (p m f s)
- Strongylidae (p)

Order *CHROMADORATA*
Family Camacolaimidae (m f s)
Plectidae (m f s)
Chromadoridae (m f s)
Order *DESMOSCOLECATA* (m)
Order *MONHYSTERATA*
Family Monhysteridae (m f s)
Linhomoeidae (m f)
Order *OXYURATA* (p)
Order *ASCARIDATA* (p)
Order *SPIRURATA* (p)
Order *FILARIATA* (p)
Order *DIOCTOPHYMATA* (p)
Order *TRICHURATA* (p)

FAMILY TRILOBIDAE

Subfamily Trilobinae

Bastiania gracilis de Man. (M).

Tripyla monohystera de Man. (M); *T. setifera* Bütschli (D); *T. papillata* Bütschli (D); (*T. affinis* de Man mentioned by Ditl. is identical with *T. papillata* Bütschl. according to Mic.)

Trilobus pellucidus Bastian (D); *T. medius* G. Schn. (M); *T. gracilis* Bastian (D); *T. grandipapillatus* Brakenhoff (D 21); *T. stefanskii* (M); *T. steineri* Mic. (M); *T. wesenbergi* Mic. (M); *T. allophysis* Steiner (M); *T. pseudallophysis* Mic (M) (according to Schneider (1939) syn. *T. helveticus* Hofm.)

Prismatolaimus dolichurus de Man (D); *P. intermedius* Bütschli (M).

Cryptonchus tristis (Ditlevsen) (D).

Mononchus niddensis Skwarra (M); *M. macrostoma* Bastian (D); *M. spectabilis* Ditlevsen (D); *M. papillatus* Bastian (D); *M. muscorum* (Duj.) (M); *M. rotundicaudatus* Skwarra; *M. brachyurus* Bütschli (D); *M. dolichurus* Ditlevsen (D).

FAMILY DORYLAIMIDAE

Subfamily Alaiminae

Alaimus elegans de Man (M); *A. dolichurus* de Man (M); *A. primitivus* de Man (M).

Subfamily Ironinae

Ironus ignavus Bastian (D).

Subfamily Tylencholaiminae

Pharetrolaimus sagittifer de Man.

Diphtherophora communis de Man.

Tylencholaimus mirabilis (Bütschli); *T. minimus* de Man (M); *T. stecki* Steiner (M).

Tylolaimophorus typicus de Man.

Subfamily Dorylaiminae

Actinolaimus macrolaimus (de Man) (D).

Dorylaimus macrodorus de Man (M); *D. limnophilus* de Man; *D. doryuris* Ditlevsen (D); *D. longicaudatus* Bütschli (D); *D. brigdammensis* de Man (D); *D. flavomaculatus* v. Linstow (M); *D. stagnalis* Duj. (D); *D. crassus* de Man (M); *D. attenuatus* de Man (M); *D. bastiani* Bütschli (D); *D. filiformis* Bastian (M); *D. hofmänneri* Menzel; *D. monhystera* de Man; *D. micoletzkyi* de Man; *D. ditlevseni* Mic. (D); *D. parvus* de Man; *D. gracilis* de Man; *D. microdorus* de Man; *D. balticus* Schulz; *D. acuticauda* de Man (D); *D. carteri* Bastian (D); *D. eurydorys* Ditlevsen (D); *D. regius* de Man; *D. rhopalocercus* de Man (D); *D. centrocercus* de Man (M); *D. bryophilus* de Man (M); *D. obtusicaudatus* Bastian (D); *D. ettersbergensis* de Man; *D. laticollis* de Man (M); *D. tritici* Bastian (M); *D. gaussi* Steiner (M); *D. czernowitziensis* Mic. (M).

FAMILY CAMACOLAIMIDAE

Aphanolaimus aquaticus v. Daday (D 21); *A. attentus* de Man;
Paraphanolaimus behningi Mic. (M).

FAMILY PLECTIDAE

Wilsonema auriculatum (Bütschli) (M); *W. tentaculatum* Fuchs; *W. otophorum* de Man.

Rhabdolaimus terrestris de Man (M).

Walcherenia typica de Man (M).

Plectus granulosus Bastian (D); *P. tenuis* Bastian (M); *P. cirratus* Bastian (incl. *P. parietinus* Bastian) (D); *P. rhizophilus* de Man (D); *P. longicaudatus* Bütschli (M); *P. communis* Bütschli; *P. geophilus* de Man (M); *P. parvus* Bastian (M).

FAMILY CHROMADORIDAE

Subfamily Cyatholaiminae

Ethmolaimus pratensis de Man (M).

Achromadora terricola (de Man) (M); *A. ruricola* (de Man) (M); *A. dubia* (Bütschli) (M).

Subfamily Choanolaiminae

Choanolaimus psammophilus de Man.

Subfamily Chromadorinae

Prochromadorella bioculata (M. Schultze) (M); *P. viridis* (v. Linstow) (M);

Punctodora ratzeburgensis (v. Linstow) (D 21).

Chromadorita leuckarti (de Man) (D).

Subfamily Desmodorinae

Prodesmodora circulata (Mic.) (M).

FAMILY MONHYSTERIDAE

Subfamily Monhysterinae

Theristus dubius (Bütschli) (M); *Th. setosus* (Bütschli) (M).

Monhystera paludicola de Man (M); *M. stagnalis* Bastian (M); *M. villosa* Bütschli; *M. agilis* de Man (M); *M. dispar* Bastian (D); *M. similis* Bütschli (D); *M. vulgaris* de Man (M); *M. filiformis* Bastian (M).

Desmolaimus brachystoma (Hofm) (M); *Cylindrolaimus communis* de Man (M).

FAMILY ANGUILLULIDAE

Subfamily Anguillulinae

Rhabditis monhystera Bütschli (M); *Rh. teres* A. Schneider; *Rh. papillosa* A. Schneider; *Rh. dolichura* A. Schneider; *Rh. filiformis* Bütschli; *Rh. elongata* A. Schneider; *Rh. longicaudata* Bastian; *Rh. brevispina* Claus (D); *Rh. pellio* Schneider (D).

Diploscapter coronata Cobb.

Subfamily Cephalobinae

Teratocephalus palustris de Man (M); *T. crassidens* de Man (M); *T. terrestris* (Bütschli (M).

Acrobeles emarginatus (de Man); *A. bütschlii* (de Man); *A. demani* Thorne; *A. vexilliger* de Man; *A. insubricus* (Steiner); *A. ciliatus* v. Linstow (D 21).

Cephalobus nanus de Man; *C. persegnis* Bastian (D); *C. filiformis* de Man; *C. striatus* Bastian (M); *C. oxyuroides* de Man; *C. elongatus* de Man (D); *C. longicaudatus* Bütschli.

Panagrolaimus rigidus (A. Schneider) (M).

Macrolaimus crucis Maupas.

Subfamily Bunoneminae

Bunonema ditlevseni Mic. (M); *B. richtersi* Jägersk.; *B. reticulatum* Richters (M).

FAMILY TYLENCHIDAE

Subfamily Diplogasterinae

Diplogasteroides variabilis Mic. (M).

Diplogaster gracilis Bütschli (D); *D. armatus* Hofm. (M); *D. fictor* Bastian (D); *D. rivalis* Leydig (D); *D. nudicapitatus* Steiner (M); *D. longicauda* (Claus) (D).

Subfamily Tylenchinae

Tylopharynx striata de Man.

Ecphyadophora tenuissima de Man.

Rotylenchus robustus (de Man) (D); *R. multicinctus* (Cobb);

Tylenchorhynchus dubius (Bütschli) (D); *T. gracilis* (de Man) (M).

Pratylenchus pratensis (de Man).

Tylenchus davainei Bastian (D); *T. agricola* de Man (M); *T. filiformis* Bütschli (M); *T. graciloides* Mic. (M); *T. brevicauda* Mic. (M).

Ditylenchus dipsaci (Kühn) (M); *D. intermedius* (de Man) (M).

Jotonchium consobrinum (de Man) (M);

Paraphelenchus pseudoparietinus Mic. (M);

Aphelenchus avenae Bastian.

Aphelenchoides parietinus (Bastian) (M).

Genuine plant parasitic species have not been included.

Subfamily Hopolaiminae

Procriconema (straleni?) de Coninck; *P. membranifer* Mic. (M).

Criconema annulifer (de Man); *C. de-mani* Mic. (M); *C. sphagni* Mic. (M). *C. rusticum* Mic.

Iota cobbi Mic. (M).

12. SUMMARY

Freeliving nematodes are of normal occurrence in the soil. They are so numerous that, beforehand, a certain importance must be ascribed to them. As it is mentioned in the introduction this has been done in several manuals although their nutrition was imperfectly known and their number was underestimated. The purpose of this paper is to present such information concerning the biology and ecology of freeliving nematodes that it becomes possible to estimate their qualitative and quantitative share in the biological processes taking place in the soil and to give a picture of their basic environmental requirements.

It appears from the historical survey that the qualitative composition of the soil fauna of nematodes is well known in some localities outside Denmark, while the quantitative statements are unreliable, the numbers being much too low except those given by *Franz* and *Stöckli* from localities in Austria and Switzerland. In addition the quantitative statements have not been given in terms of weight apart from rather loose suggestions. Seasonal variations have only been found in the locality investigated by *Seidenschwarz*. They could not be demonstrated in my localities. The faunas of different localities have been compared by several authors and it turns out that most species are common to several types of localities, while a few seem to be restricted to specific soils. The vertical distribution has not been studied especially but the statements present seem to indicate that it corresponds to that of most other soil microorganisms. The moisture relations are known in principle but have often been neglected. The respiratory metabolism is completely unknown. The nutrition is only known from occasional observations. Culture experiments have only been performed with defined food in plant parasitic species, *Rhabditis spp.* and *Diplogaster spp.* besides *Mononchus* and a few other predatory genera. The reproductive rate is known from experimental conditions in some species. Thus the importance of nematodes has been discussed on the basis of unreliable suppositions.

In order to permit an estimation of the importance of nematodes it was necessary to supplement much of the previous knowledge and to acquire new information on several questions hitherto unanswered. The material and methods used for this paper are described in chapter 3.

A wide range of localities was selected covering most soil types of importance in this country with due regard to soil structure and vegetation, in natural as well as cultivated soils. A material amounting to ca. ca. 350 000 nematodes, of which ca. 205 000 originate from the localities analysed in this paper, has served as a basis for my investigation. They were obtained by extraction from a large number of samples by means of a new technique described in a previous paper. The efficiency of the extraction was estimated at ca. 90 %. The density of the

fauna is given in terms of number and weight per sq. m. A direct weighing would introduce large errors, thus resort was taken to the fact that the cross section of nematodes is exactly circular. This allowed a fairly exact determination of the volume. Two procedures were elaborated, one for the more exact determinations in connection with the statements of oxygen consumption per unit weight (involving a determination of the specific gravity) and one for statement of weight per sq. m. of soil. Average weight of the most important soil nematodes is given in table 1, it ranges from ca. 0.02 — 56 γ i. e. a size difference of 2800 times is found between different species. The oxygen consumption was measured by means of the diver technique of *Holter* and *Linderstrøm-Lang*, which turned out to be excellent for the purpose, allowing one to measure the consumption of a single individual of the large species and of a few individuals of the small ones. A technique was elaborated for the culture of several species and for obtaining sterile eggs.

Chapter 4 gives a survey of the fauna in various localities ranging from pure sand via clay to organic soils and from extremely dry via optimum to permanently moist mineral and organic soil. The results from all the localities are presented in tables 2—16. Cultivated soil was also examined.

The general distribution of the fauna as based upon the single localities is discussed in chapter 5. The distribution of the ca. 100 species met with confirms the concept that a very large proportion of the species are eurytopic and common to all the soil types. On a weight basis it constitutes ca. 95 % of the fauna in sand and raw humus when extreme localities are left out of consideration. In permanently moist soil — mineral as well as organic — the eurytopic component is much less important, ca. half of the weight in such localities being constituted by typical freshwater species not occurring in soils of smaller water content. In sand and raw humus a stenotopic group is present confined to these soil types. Each of them consists of three species, which constitute only ca. 3 % of the weight in most localities. In extremely dry sand the stenotopic "sand fauna" increases in importance. For my purposes this type of distribution means that the main stress may be laid upon the eurytopic group except in permanently moist localities.

The vertical distribution of the fauna is discussed in chapter 6. The general concept that nematodes are confined to the upper 20—30 cm of the soil was confirmed in most localities. However, a very deviating type of distribution was found on the shore beach. Here two nematode maxima were demonstrated one 10—20 cm below the surface and a lower maximum 10—30 cm above the ground water table (which is located at ca. 80 cm depth) (see fig. 4) In most other localities the lower maximum is probably absent, at least no nematodes are present in this depth on "the Plain", a permanent pasture 500 m

from the shore. The distribution of nematodes within the upper maximum is different according to the locality. In most soils with a plant cover the number decreases from the surface downwards (as found by most authors). In cultivated soil the decrease is less abrupt, and in localities which are extremely dry or without a plant cover a maximum is found 3—6 cm below the surface, the number decreasing upwards as well as downwards. A knowledge of the vertical distribution is necessary when it is desired to choose a sampling yielding the same proportion of the total fauna, which was necessary in my case.

The moisture relations of the soil microfauna. The concept of a "microfauna" must, in an ecological sense be defined on the basis of the relation between the size of the animals and the size of the structural elements of the soil in which they live. The microfauna does not exert a mechanical influence upon the structure of the soil, in contrast with the macrofauna. Within the microfauna two components may be distinguished: an aerophilous, the medium of which is the air phase of the soil (mites and collembola) and a hydrophilous, which utilizes the water phase as a medium (protozoa, turbellarians, nematodes, rotifers, tardigrades). On the basis of statements in the literature it is emphasised, that only a fraction of the total amount of water present in the soil is accessible to the microfauna. The fact that the aerophilous and hydrophilous animals have different water requirements, is demonstrated by discussing their different distribution in some localities. In the hydrophilous animals we must distinguish a freshwater and a soil fauna, in the aerophilous a dry soil and a moist soil fauna. The fact that the nematode fauna becomes poorer when the water content increases to permanently moist, does not invalidate the point of view that nematodes are in principle aquatic animals (see fig. 6), as the fauna of freshwater and sea bottom is also much poorer than that of most soils; it is explained by differences in the supply of food. Several morphological and physiological features enables the nematodes to live successfully in the soil, which is an ever shifting biotope: small size, slender body shape, type of locomotion and the power to survive desiccations in an anabiotic state may be mentioned.

The oxygen consumption of nematodes as measured at 16° C ranges from ca. 600—1500 cc per kg per hour and it tends to decrease with increasing size of the species although exceptions occur. It is largely independent of variations in the 0_2-tension occurring in the soil and of the food content of the gut. The influence of locomotion is very slight in accordance with the fact, that the true work performed is small. Juvenile (small) individuals have a higher respiratory rate than adult while the size is not found to exert a significant influence when only adult individuals are considered. The same applies to the sex. The influence of temperature is great. The temperature metabolism curve obtained corresponds nearly to that compiled by *Krogh* for coldblooded vertebrates.

With regard to nutrition four groups are distinguished: 1. The *Tylenchinae* suck plant roots in some cases perhaps also fungi. This is well established in the literature. The group was not especially studied but it was shown that bacteria are not sufficient nutrition for 5 species of *Tylenchinae* as they do not allow reproduction although the species can be maintained on bacteria as sole food for long time. 2. The nutrition of the *Dorylaiminae* could not be elucidated with certainty. They could be maintained for long time on algae and indications are at hand from direct observation that algae are an important constituent of the food in natural localities. However, the reproductive rate was so low under experimental conditions that I have hesitated to decide the question definitely. The presence of a stylet in these two groups indicate that the food is obtained by suction. 3. A large group (*Achromadora, Wilsonema, Plectus, Cephalobus, Acrobeles, Teratocephalus, Panagrolaimus, Macrolaimus, Rhabditis, Alaimus, Bunonema* and probably also *Ethmolaimus*) feed on particulate food, especially bacteria. They cannot live in sterile filtrates of bacterial cultures nor in sterile soil or soil suspensions or heat killed bacteria, while sterile eggs transferred to a suspension of bacterial pure cultures in sterile water allowed growth and reproduction of several generations. In addition bacteria were demonstrated in the gut of individuals from natural localities. Bacterial food was hitherto known in *Rhabditis* and *Diplogaster*. In all the genera mentioned except *Alaimus* rasping plates or teeth enable the animals to crush the food. The masticatory apparatus may consist of teeth in the mouth cavity, valves in the oesophageal bulb (acting like the mastax of rotifers) or valves and a rasping plate in the oesophageal bulb. The dimension of the teeth is of the order of size a few μ corresponding to the size of the particles. 4. According to the literature *Mononchus* and *Tripyla* are predators, to this group must be added *Choanolaimus*. All of them feed on protozoa, rotifers, nematodes or other animals. Teeth — much larger than those of the preceding group — are present in the mouth cavity or the oesophagus.

The reproductive rate for some species is given in table 24 as found under experimental conditions. They are of the same order as those given by *Maupas*. Generally ca. 20 days elapse between two subsequent generations, in *Rhabditis* only ca. 5 and in some large species upwards of 50. These values cannot be applied directly to nature but they may give an idea of the sequence of generations. The eggs are large in comparison with the size of the species. A single individual of *Cephalobus elongatus* deposited (in culture) 209 eggs within 22 days i. e. 500 % of the weight of the mother.

On the basis of these premises certain conclusions are drawn in chapter 10. Firstly the distribution of nematodes is discussed, not as single species but as ecological units based upon the nutrition. Table 25 gives the primary material expressed as total number, weight and respiration of nematodes per sq. m. in all

the localities of chapter 4 and the percentage importance of the five nutritional groups. The number of nematodes in not permanently moist mineral soil ranges from 175 000—20 000 000 per sq. m. corresponding to a weight of 0.7—17.8 g and a respiration of 0.6—17.3 cc 0_2 per sq. m. per hour at 16° C. The highest number was found in grass fields and the lowest in extremely dry localities. In raw humus and permanently moist localities the fauna is much poorer never exeeding 3 000 000 individuals and 5 g per sq. m. In freshwater (based upon *Micoletzky* 1925)) alga feeders and predators are the most important groups while root suckers are almost absent. In permanently moist soil the importance of predators decreases considerably, the most important group being the alga feeders. The importance of bacteria feeders and root suckers increases. In ordinary soil the importance of bacteria feeders rises considerably, alga feeders still being important while the root suckers have now increased to ca. 10 % of the total weight (here it must be remenbered that the very numerous obligate plant parasites have not been considered in this paper). In extremely dry soil the alga feeders constitute the greater part of the very poor fauna.

The importance of nematodes is next discussed partly in comparison with other organisms and in relation to the nitrogen cycle of the soil. The food cycle of nematodes is given in fig. 16. The only nutritional group of nematodes which can be discussed singly as yet is the one feeding upon bacteria. A conclusion as to the importance of these species was obtained by ascribing to them an importance of the order of 10 % of that of protozoa. A final conclusion cannot be obtained as yet, but certain probabilities are discussed as to the way in which they may influence the bacterial number and activity and the total microbiological activity. The competition for basic nutrients may be very intense in the soil, the microflora and the higher plants being involved in it. This makes conditions very complex. The soil fauna plays a certain role in acting as a reserve of easily available nutrients which is mobilized during the activity of the animals or subsequent to their death. Even if part of their nutrition is obtained from a closed circuit they may increase the tempo of mineralization in causing a renewed circulation of the nutrients bound in the microflora, which constitute ca. 80 % of the total weight of organisms in a mineral soil. The gross importance of nematodes in this mobilization is calculated on the basis of the oxygen consumptions assuming that they feed upon some sort of protoplasm. It turns out that the amount of nitrogen combusted by nematodes equals 1—27 kg per ha per vegetation period of 100 days. In the rye field at Studsgaard the amount of nitrogen combusted by nematodes equals 3—5 kg i. e. ca. 10 % of the amount absorbed by the crop and the annual values are still higher. When it is remembered that nematodes constitute ca. 1 % only of the total fauna, the influence of the soil fauna on the whole cannot be neglected.

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DANSK SAMMENFATNING

De fritlevende nematoder er et normalt faunaelement i jorden. De er så talrige, at der på forhånd må tilskrives dem en vis betydning. Som omtalt i Indledningen er dette blevet gjort i adskillige håndbøger endskønt deres ernæring kun har været ufuldstændig kendt og deres antal undervurderet. Formålet med dette arbejde er at give sådanne oplysninger vedrørende de fritlevende nematoders biologi og økologi, at det bliver muligt at skønne deres kvalitative og kvantitative andel i de biologiske processer, der forløber i jorden, og at give et indtryk af deres fundamentale milieukrav.

Det fremgår af den historiske oversigt, at den kvalitative sammensætning af nematodfaunaen i jorden er velkendt i en del lokaliteter udenfor Danmark, mens de kvantitative angivelser er upålidelige, idet antallet har været for lavt, når undtages resultaterne, der er opnået af *Franz* og *Stöckli* fra lokaliteter i Østrig og Schweiz. Hertil kommer, at de kvantitative angivelser ikke har været baseret på vægt bortset fra nogle ganske løse skøn. Sæsonvariationer i antallet blev fundet af *Seidenschwarz*, men de kunne ikke påvises i mine lokaliteter. Faunaen i forskellige lokaliteter er blevet sammenlignet af adskillige forfattere, og det har vist sig, at de fleste arter forekommer i adskillige lokalitetstyper, idet dog nogle enkelte synes at være begrænset til visse jorde. Den vertikale udbredelse har ikke været genstand for specielle undersøgelser, men de angivelser, der findes i litteraturen, synes at vise, at den svarer til de fleste andre jordbundsorganismers. Fugtighedskravene kendes i princippet, men er ofte blevet overset. Det respiratoriske stofskifte er fuldstændig ukendt. Ernæringen er kun kendt fra tilfældige iagttagelser. Dyrkningsforsøg er — på basis af vel defineret føde — kun gjort med visse planteparasitiske arter, *Rhabditis spp.* og *Diplogaster spp.* samt *Mononchus spp.* og nogle få andre slægter, der ernærer sig som rovdyr. Forplantningsintensiteten er kendt hos nogle arter under experimentelle betingelser. Nematodernes betydning er således blevet diskuteret på basis af utilstrækkelige forudsætninger.

Med henblik på en beregning af nematodernes betydning var det således nødvendigt at supplere meget af det tidligere kendte og at fremskaffe oplysninger om adskillige spørgsmål, der hidtil var forblevet ubesvarede. Materialet og metodiken, der er benyttet i dette arbejde, er beskrevet i kapitel 3.

Et alsidigt udvalg af lokaliteter benyttedes som repræsentanter for de vigtigste danske jordtyper under hensyntagen til jordens struktur og vegetationen på naturlige såvel som dyrkede jorde. Som grundlag for undersøgelserne har tjent et materiale på ca. 350 000 nematoder, af hvilke ca. 205 000 er direkte indgået i dette arbejde. De samledes ved uddrivning fra et stort antal prøver ved hjælp af en ny teknik, der er beskrevet i et tidligere arbejde *(Overgaard* (1948 a)). Uddrivningen er ca. 90 % effektiv. Faunaens tæthed er angivet som antal og vægt pr. m². En direkte vejning ville medføre store fejl, i stedet benyttedes derfor en

beregning af volumen på basis af det forhold, at nematoder i tværsnit er absolut circulære, hvorved en ret nøjagtig beregning lader sig gøre. Der udarbejdedes to metoder, en mere nøjagtig i forbindelse med måling af iltforbrug pr. vægtenhed (kombineret med en vægtfyldebestemmelse) og en anden i forbindelse med angivelse af vægtmængde nematoder pr. m^2 jord. Gennemsnitsvægten af de mest betydende nematoder er givet i tabel 1, den varierer fra ca. 0.02—56 γ d. v. s. en størrelsesforskel på 2800 gange. Iltforbruget måltes ved hjælp af dykkertekniken *(Holter* og *Linderstrøm-Lang)*, der viste sig at være fortræffelig for formålet, idet den tillod at måle forbruget for et enkelt individ af de store arter og for nogle få individer af de små arter. En speciel dyrkningsteknik udarbejdedes for en del arter samt en metode til opnåelse af sterile æg.

Kapitel 4 giver en oversigt over faunaen i forskellige lokaliteter fra rent sand over ler til organiske jorde og fra extremt tørre over optimale til permanent fugtige mineralske og organiske jorde. Resultaterne fra alle lokaliteterne er givet i tabellerne 2—16. Dyrkningsjord er også blevet undersøgt.

Faunaens almindelige udbredelse baseret på de enkelte lokaliteter diskuteres i kapitel 5. Udbredelsen af de ca. 100 arter bekræfter den opfattelse, at en meget stor del af arterne er eurytope og fælles for alle jordtyperne. På vægtbasis udgør de eurytope arter ca. 95 % af faunaen i sand og råhumus, når de extreme lokaliteter lades ude af betragtning. I konstant fugtige jorde — mineralske såvel som organiske — er denne eurytope gruppe meget mindre betydende, idet ca. halvdelen af vægten i sådanne lokaliteter udgøres af typiske ferskvandsarter, der ikke forekommer i jord af mindre fugtighedsgrad. I sand og råhumus findes en for hver af disse jordtyper karakteristisk stenotop artsgruppe. Hver af disse består af 3 arter, som kun udgør ca. 3 % af vægten i de fleste lokaliteter. I extremt tørt sand tiltager den stenotope »sand fauna« i betydning. For dette arbejdes vedkommende betyder denne udbredelsestype, at hovedvægten kan lægges på den eurytope gruppe undtagen i konstant fugtige lokaliteter.

Faunaens vertikale udbredelse diskuteres i kapitel 6. Den almindelige opfattelse, at nematoderne kun forekommer i de øverste 20—30 cm, bekræftedes i de fleste lokaliteter. På en sandstrandslokalitet fandtes imidlertid en meget afvigende vertikal udbredelsestype. Der fandtes her 2 nematodmaxima: eet 10—20 cm under overfladen og eet 10—30 cm over grundvandstanden (der findes i ca. 80 cm dybde) (se fig. 4). I de fleste andre lokaliteter mangler det nedre maximum sandsynligvis, i det mindste fandtes ingen nematoder i denne dybde på »Sletten«, et græsningsareal 500 m fra stranden. Fordelingen af nematoderne indenfor det øvre maximum er forskellig fra den ene lokalitet til den anden (se fig. 5). I de fleste lokaliteter med et plantedække aftager tallet fra overfladen og nedefter som fundet af de fleste forfattere. I dyrkningsjord aftager det langsommere og i lokaliteter, der er extremt tørre eller uden plantedække

findes et maximum 3—6 cm under overfladen, således at antallet aftager både opefter og nedefter. Et kendskab til den vertikale fordelingstype er nødvendig for valget af en prøvedybde, der giver den samme brøkdel af den totale fauna i forskellige lokalitetstyper.

Jordmikrofaunaens fugtighedsforhold. Begrebet »mikrofauna« må i økologisk henseende defineres på basis af forholdet mellem størrelsen af dyrene og jordens strukturelementer. Mikrofaunaen øver ikke nogen mekanisk indflydelse på den omgivende jords struktur. I denne henseende står den i modsætning til makrofaunaen. Indenfor mikrofaunaen må der skelnes mellem to komponenter: en aerophil, hvis medium er jordens luftfase (mider og collemboler) og en hydrophil, der udnytter vandfasen som medium (protozoer, turbellarier, nematoder, rotatorier og tardigrader). På basis af literaturkilder understreges det, at det for mikrofaunaen tilgængelige vand kun udgør en brøkdel af den totalt tilstedeværende vandmængde. Det forhold, at den aerophile og den hydrophile mikrofauna stiller forskellige krav til vandføringen diskuteres under henvisning til deres forskellige udbredelse i forskelligartede lokaliteter. For de hydrophile dyrs vedkommende må der skelnes mellem en ferskvandsfauna og en jordfauna. for de aerophiles mellem en fugtigbundsfauna og en tørbundsfauna. Der findes en tendens til at nematodfaunaen bliver fattigere når jordens vandindhold stiger til konstant fugtigt. Dette afkræfter dog ikke den anskuelse, at nematoderne principielt må betragtes som aquatiske dyr (se fig. 6), eftersom nematodfaunaen i både fersk- og saltvand også er fattigere end i de fleste jordtyper. Forholdet forklares udfra forskelle i ernæringssituationen. Adskillige morfologiske og fysiologiske træk muliggør nematodernes rige forekomst i jorden, der er et stadigt skiftende milieu: lille størrelse, slank form, bevægelsesmåde og evnen til at overleve udtørringer i en anabiotisk tilstand.

Nematodernes iltforbrug målt ved 16° C varierer fra ca. 600—1500 cc pr. time og det tenderer mod at aftage med tiltagende størrelse, når de forskellige arter sammenlignes, idet der dog findes undtagelser. Iltforbruget er i udstrakt grad uafhængigt af ilttensionen (indenfor de variationer, der findes i jorden) og af tarmens fødeindhold. Bevægelsens indflydelse er meget lille i overensstemmelse med, at det reele arbejde, der udføres, er lille. Unge individer har højere stofskifteniveau end voksne af samme art, mens størrelsen ikke fandtes at øve påviselig indflydelse når kun voksne individer sammenlignedes. Forskelle i iltforbruget hos de to køn kunne heller ikke påvises. Temperaturens indflydelse på stofskiftet er stor, idet temperatur-stofskiftekurven svarer nært til den, *Krogh* har sammenstillet for koldblodede hvirveldyr.

Med hensyn til ernæringen må der skelnes mellem 4 grupper: 1. *Tylenchinae* suger på planterødder og i nogle tilfælde måske også svampehyfer. Dette er velkendt fra litteraturen. Denne gruppe har ikke været gjort til genstand for spe-

cielle undersøgelser i dette arbejde, men det vises dog, at bakterier ikke er sufficient næring for 5 arter *Tylenchinae*, idet der ikke skete nogen formering selv om arterne kunne dyrkes på exclusiv bakteriekost gennem lang tid. 2. Indenfor *Dorylaiminae* kunne næringen ikke fastslås med sikkerhed. Visse arter kan holdes gennem lang tid på alger, og en direkte iagttagelse tyder på, at alger er et betydende næringsemne i naturlige omgivelser. Imidlertid er forplantningsintensiteten under experimentelle omstændigheder så lav, at spørgsmålet ikke har kunnet afgøres med sikkerhed. Tilstedeværelsen af en stilet hos begge disse grupper viser, at næringen optages ved sugning. 3. En stor gruppe (*Achromadora, Wilsonema, Plectus, Cephalobus, Acrobeles, Teratocephalus, Panagrolaimus, Rhabditis, Alaimus, Bunonema* og sandsynligvis også *Ethmolaimus* lever af partikulær føde, især bakterier. De kan ikke leve i sterile filtrater af bakteriekulturer, heller ikke i steril jord eller jordsuspensioner eller i en opslemning af varmedræbte bakterier. I modsætning hertil var klækning, vækst og formering normal efter overførelse af sterile æg i en suspension af bakterier i sterilt vand. Endvidere er der påvist bakterier som normalt tarmindhold i nematoder stammende fra naturlige omgivelser. At bakterier tjener som næring var hidtil kun kendt fra *Rhabditis* og *Diplogaster spp.* Hos alle de omtalte slægter undtagen *Alaimus* findes der raspeplader eller tænder, der tillader dem at knuse føden. Tyggeapparatet kan bestå af tænder i mundhulen, klapper i oesophagus bulbus (virkende som mastax hos rotatorierne) eller klapper og raspeplader i oesophagus bulbus. Tænderne er af størrelsesordnen nogle få μ svarende til partiklernes størrelse. 4. Ifølge litteraturen er *Mononchus* og *Tripyla* rovdyr. Til denne gruppe må føjes *Choanolaimus*. De lever alle af protozoer, rotatorier, nematoder eller andre dyr. Tænder — meget større end dem der træffes hos den foregående gruppe — findes i mundhulen eller oesophagus.

Forplantningsintensiteten for nogle arter er givet i tabel 24, således som den fremgik af dyrkningsforsøgene. Den er af samme størrelsesorden som *Maupas* har fundet. Sædvanligvis går der ca. 20 dage mellem æglægning i to på hinanden følgende generationer, hos *Rhabditis* dog kun ca. 5 og hos nogle store arter op mod 50. Disse angivelser kan ikke overføres direkte til forholdene i naturen men kan dog bibringe en forestilling om den hastighed, hvormed generationerne følger efter hinanden. Et enkelt individ af *Cephalobus elongatus* aflagde i kultur 209 æg indenfor 22 dage, d. v. s. ca. 500 % af moderens egen vægt.

På basis af de foregående specialundersøgelser drages der i kapitel 10 visse konklusioner. Først diskuteres udbredelsen af nematoderne, ikke som enkelte arter men som økologiske enheder i henseende til ernæring. Tabel 25 giver primærmaterialet udtrykt som total antal, vægt og respiration pr. m^2 i alle lokaliteterne fra kapitel 4 og den procentiske betydning af de fire ernæringsgrupper samt en femte gruppe, hvis næringskrav ikke er kendt med sikkerhed. Nemato-

dernes antal i ikke konstant fugtige mineraljorde varierer fra 175 000 til 20 000 000 pr. m^2 svarende til en vægt af 0,7—17,8 g og en respiration på 0,6—17,3 cc 0_2 pr. time ved 16° C. Det største antal findes i græsmarker og det laveste i extremt tørre lokaliteter. I råhumus og konstant fugtige lokaliteter er faunaen meget fattigere, idet den aldrig overstiger 3 000 000 individer = 5 g pr. m^2. I ferskvand (på basis af *Micoletzky* (1925)) er algeædere og rovdyr de vigtigste grupper, mens rodsugere næsten mangler. I konstant fugtig jord falder rovdyrenes betydning stærkt, således at algeæderne bliver den vigtigste gruppe, idet dog bakterieædere og rodsugere tiltager i antal. I normal jord stiger bakterieædernes antal betydeligt, algeæderne er stadig betydende, mens rodsugernes andel er steget til ca. 10 % af den totale vægt, idet det dog her må erindres, at de obligate planteparasiter er ladt ude af betragtning i dette arbejde. I extremt tørt jord udgør algeæderne størstedelen af den meget fattige fauna.

Nematodernes betydning diskuteres derefter dels i sammenligning med andre organismer og dels i relation til kvælstofkredsløbet i jorden. Nematodernes ernæringsmæssige placering blandt en del andre organismer fremgår af fig. 16. Den eneste ernæringsgruppe der på nuværende tidspunkt kan diskuteres isoleret er den, der lever af bakterier. Dens indflydelse på bakteriefloraen i jorden anslås til at være af størrelsesordnen 10 % af den, protozoerne udøver. Mere detaillerede slutninger kan ikke drages på nuværende tidspunkt, men der gives en diskussion af de måder, hvorpå nematoderne kan tænkes at påvirke bakteriernes antal og aktivitet samt den totale mikrobiologiske aktivitet. Konkurrencen om de fundamentale næringsstoffer i jorden kan være meget hård og både mikrofloraen og de højere planter deltager i den. Dette gør forholdene meget indviklede. Jordfaunaen spiller en vis rolle ved at fungere som en reserve af lettilgængelige næringsstoffer, der mobiliseres under deres aktivitet og efter deres død. Selvom en del af dens næring tages fra et lukket kredsløb, kan den dog accelerere mineraliseringstempoet ved at bevirke en fornyet circulation af de næringsstoffer, der er bundet i mikrofloraen, som udgør ca. 80 % af den totale vægt af organismerne i mineraljorde. Nematodernes betydning for denne mobilisering beregnes på basis af iltforbruget under antagelse af, at de lever af protoplasma under en eller anden form. Det viser sig da, at den kvælstofmængde, der forbrændes af nematoder andrager 1—27 kg per ha pr. vegetationsperiode (à 100 dage). I en rugmark ved Studsgaard udgjorde den forbrændte kvælstofmængde 3—5 kg d. v. s. ca. 10 % af den mængde, rugafgrøden optager fra jorden, og de årlige værdier er naturligvis endnu større. Når det erindres, at nematoderne kun udgør ca. 1 % af den totale fauna, kan den samlede jordfaunas betydning ikke negligeres.

Erratum

p. 110 line 5: 73.04, read 35.53

TABLES